BULLETIN 155

A ZOOGEOGRAPHICAL STUDY OF THE AMPHIBIANS AND REPTILES OF EASTERN CANADA

BY

J. SHERMAN BLEAKNEY

1958

NATIONAL MUSEUM OF CANADA
DEPARTMENT OF NORTHERN AFFAIRS AND NATIONAL RESOURCES

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BULLETIN No. 155
BIOLOGICAL SERIES No. 54

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Issued under the authority of
THE HONOURABLE ALVIN HAMILTON
Minister of Northern Affairs and National Resources
Ottawa

1958

Price: $2.00 *Cat. No. R-93-155*

Available from the Queen's Printer, Ottawa, Canada

50788-9—1

EDMOND CLOUTIER, C.M.G., O.A., D.S.P.
QUEEN'S PRINTER AND CONTROLLER OF STATIONERY
OTTAWA, 1958

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A ZOOGEOGRAPHICAL STUDY OF THE AMPHIBIANS AND REPTILES OF EASTERN CANADA

INTRODUCTION

Amphibians and reptiles comprise an important major segment of the vertebrate fauna of Canada: major in the sense of numbers of individuals; important in the sense of economic value. The number of insects, other invertebrates, small vertebrates, and especially rodents, that these animals consume during a summer season is astronomical and is evidence of their economic value to Canadian agriculture and forestry. An example is Buckner's 1952 report on the predation of larch sawfly by frogs. It is also apparent that they themselves present a diverse and plentiful source of food for other creatures.

However, in spite of this vital position which the amphibians and reptiles hold in our fauna, their position in our literature has been obscure. There have been published many "nature observations," a number of range extensions, and a few local check lists, but no zoogeographical studies nor taxonomic studies. Up to August of 1955 (Logier and Toner, 1955) no comprehensive check list with distribution maps of Canada's herpetofauna was in existence. The maps and taxonomic works prepared by United States workers are, for the most part, inaccurate where the species concerned range into Canada. The crux of the problem is that so little specific collecting of amphibians and reptiles has been done in Canada that specimens upon which distributional and taxonomic studies could be based were not available previous to my work. A brief example will illustrate. The Painted Turtle, *Chrysemys picta*, a ubiquitous North American species of pond turtle, is common in certain sections of New Brunswick and Nova Scotia, yet until one specimen was sent from Nova Scotia to the National Museum of Canada in 1934, herpetologists of the period did not realize that the range of this species in Eastern Canada extended east of the Richelieu River in southern Quebec. Regrettably, this information did not reach chelonologists in the United States for some time, and Pope's "Turtles of the United States and Canada," printed in 1949, excluded *Chrysemys picta* from the Maritime Provinces. A similar lack of information is apparent in Carr's 1952 "Handbook of Turtles of United States, Canada, and Baja California," where the line designating range limit of the Painted Turtle in Eastern Canada is much too far *north* of the actual distribution of this species as determined by my own surveys in that area.

Field work was carried out in Nova Scotia, New Brunswick, Prince Edward Island, Quebec, and parts of eastern Ontario from 1950 through the summer of 1956 with a total of about 6,000 specimens collected. Map 1 indicates sites where collections were made.

The original purpose of my work was to discover what species of amphibians and reptiles occur in Eastern Canada and to define accurately their distributional limits. This survey has subsequently expanded in scope, and the findings may now be classified under (1) new distribution records, (2) zoogeographic patterns, (3) taxonomic aspects, and (4) life-history observations. Only the first two items of this original information will be discussed in this paper.

In all, there are 43 species and subspecies involved, and as is inevitable, the amount of material gathered for each varies considerably. In spite of the amount of information accumulated over the past seven years, more questions have been raised than answered, and these rather interesting problems will comprise a section unto themselves toward the end of this paper.

The nomenclature is that of K. P. Schmidt's 1953 "A Check List of North American Amphibians and Reptiles," which was issued by the American Society of Ichthyologists and Herpetologists. The present-day accepted procedure in herpetology is to eliminate the use of parentheses around the describer's name in cases where the genus has been changed since the species was named. The present writer takes exception to the treatment of the Common Toad and the Wood Frog in this check list and has reduced *Bufo terrestris americanus* and *B. t. copei* to *B. americanus*, and *Rana sylvatica sylvatica* and *R. s. cantabrigensis* to R. *sylvatica* (*See* Logier and Toner, 1955, for a similar viewpoint). A phylogenetic list of the amphibians and reptiles of Eastern Canada follows.

Phylogenetic List

Class: Amphibia

Order: Caudata

Family: Proteidae

Necturus maculosus maculosus Rafinesque—Mudpuppy

Family: Ambystomidae

Ambystoma jeffersonianum Green—Jefferson's Salamander

Ambystoma maculatum Shaw—Spotted Salamander

Family: Salamandridae

Diemictylus viridescens viridescens Rafinesque—Red-spotted Newt

Family: Plethodontidae

Desmognathus fuscus fuscus Rafinesque—Dusky Salamander

Plethodon cinereus cinereus Green—Red-backed Salamander

Hemidactylium scutatum Schlegel—Four-toed Salamander

Gyrinophilus porphyriticus porphyriticus Green—Purple Salamander

Eurycea bislineata bislineata Green—Two-lined Salamander

Order: Salientia

Family: Bufonidae

Bufo americanus Holbrook—Common Toad

Family: Hylidae

Hyla crucifer crucifer Wied—Spring Peeper
Hyla versicolor versicolor LeConte—Common Tree Frog
Pseudacris nigrita triseriata Wied—Swamp Cricket Frog

Family: Ranidae

Rana catesbeiana Shaw—Bullfrog
Rana clamitans Latreille—Green Frog
Rana septentrionalis Baird—Mink Frog
Rana sylvatica LeConte—Wood Frog
Rana pipiens pipiens Schreber—Leopard Frog
Rana palustris LeConte—Pickerel Frog

Class: Reptilia

Order: Chelonia

Family: Chelydridae

Chelydra serpentina serpentina Linnaeus—Snapping Turtle

Family: Kinosternidae

Sternotherus odoratus Latreille—Musk Turtle

Family: Emydidae

Clemmys guttata Schneider—Spotted Turtle
Clemmys insculpta LeConte—Wood Turtle
Emys blandingi Holbrook—Blanding's Turtle
Graptemys geographica LeSueur—Map Turtle
Chrysemys picta picta Schneider—Eastern Painted Turtle
Chrysemys picta marginata Agassiz—Central Painted Turtle

Family: Chelonidae

Lepidochelys olivacea kempi Garman—Atlantic Ridley Turtle
Caretta caretta caretta Linnaeus—Atlantic Loggerhead Turtle

Family: Trionychidae

Trionyx ferox spinifera LeSueur—Spiny Soft-shelled Turtle

Family: Dermochelidae

Dermochelys coriacea coriacea Linnaeus—Atlantic Leatherback Turtle

Order: Sauria

Family: Scincidae

Eumeces fasciatus Linnaeus—Blue-tailed Skin

Order: Serpentes

Family: Colubridae

Natrix sipedon sipedon Linnaeus—Northern Water Snake
Storeria dekayi dekayi Holbrook—DeKay's Snake

Storeria occipitomaculata occipitomaculata Storer—Red-bellied Snake
Thamnophis sauritus sauritus Linnaeus—Ribbon Snake
Thamnophis sirtalis sirtalis Linnaeus—Eastern Garter Snake
Diadophis punctatus edwardsi Merrem—Eastern Ring-necked Snake
Coluber constrictor constrictor Linnaeus—Black Racer
Opheodrys vernalis vernalis Harlan—Eastern Smooth Green Snake
Elaphe vulpina gloydi Conant—Eastern Fox Snake
Elaphe obsoleta obsoleta Say—Pilot Black Snake
Lampropeltis doliata triangulum Lacepede—Eastern Milk Snake

Acknowledgments

The author is indebted to a great many persons and organizations for their assistance during the seven years that this study was pursued. He gratefully acknowledges the instruction, advice, and criticism received from Dr. M. J. Dunbar, his academic supervisor.

He wishes to acknowledge in particular the Nova Scotia Museum of Science, the Carnegie Corporation of New York (Carnegie Arctic Scholarship, 1951-52), and the National Museum of Canada, as the three organizations which financed the extensive field studies conducted in Eastern Canada. The writer is also indebted to the Hollinger-Ungava Airlines at Seven Islands, Quebec, for donating free airline transportation over southern Quebec and Labrador during the summer of 1952.

Valuable field assistance has been rendered by L. Stickles, D. J. Osborn, Dr. G. A. Schad, F. R. Cook, and S. Gorham. J. L. Martin, H. White, E. B. S. Logier, and Dr. C. E. Hall generously provided valuable information and unpublished records. B. S. Wright kindly supplied laboratory space, a canoe, and a guide during the survey of the Grand Lake area in New Brunswick. In addition, the author's wife assisted greatly both in the field and during the preparation of this manuscript.

REVIEW OF LITERATURE

Herpetological writings that concern Eastern Canada are for the most part distributional in nature and limited to brief notes and local check lists and are to be found in the Bibliography of Eastern Canadian Distribution Reports at the end of this paper. Only the more inclusive contributions, which in actuality summarize the briefer notes, will be considered in this review.

The questionable reports that are mentioned in this review are discussed in detail in the section entitled "Rare or Questionable Reports."

Eastern Canada

Beginning with those papers which concern broad regions of Eastern Canada, the writings of Philip Cox, of New Brunswick, are the earliest. He collected in Gaspé, New Brunswick, Prince Edward Island, and Nova Scotia, and reported his findings in 1899. In 1907 he published an annotated list of lizards and salamanders of Canada, but the emphasis was on his own personal experience with the various species in the Maritime Provinces and Gaspé.

The next major contribution to regional herpetology in Canada was not made until 1942 when the first list of the amphibians and reptiles of Canada, a total of 96 forms, was published by Logier and Toner of the Royal Ontario Museum. They did not, however, attempt to delimit the ranges of any of the species. Many of the subspecies are not now recognized, and several new species have been discovered since then. The latest total of species and subspecies stands at 100.

Soon after, in 1948, R. C. Mills compiled a check list of amphibians and reptiles for Canada, with descriptions of known ranges of each species. These ranges were based on all the records, both published and unpublished, that Mills could locate. Unfortunately, he quoted only a few of these sources, so it is impossible to check the original specimens or descriptions.

A paper entitled "An Analytical Study of the Geographic Distribution of *Rana septentrionalis*" was written by J. A. Moore in 1952. It is the only herpetological study that includes Eastern Canada in its scope. However, several of his conclusions are invalid because he believes that this species ranges only to latitude 50°N., whereas it actually occurs as far north as latitude 57°30′N. In addition he had no records from the provinces of New Brunswick, Nova Scotia, or Prince Edward Island.

In 1952 Wright and Wright produced a monumental paper listing by state and province all the different species of snakes that have been reported in North America. Each province is given an accredited list and a problematic list, but it is only in the latter that the occasional reference is given.

In this same year, Clarke, Irwin and Company published E. B. S. Logier's book, "The Frogs, Toads and Salamanders of Eastern Canada." It is primarily written for the general public but does have keys, illustrations of each species, and a description of the distribution of each form. Some of these distributional limits have become obsolete as a consequence of my own work in Eastern Canada, but the book otherwise stands as a

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cornerstone in Canadian herpetological literature because of its scope, keys, illustrations, and sound taxonomic discussions (particularly on *Bufo americanus* and *Rana sylvatica*).

E. B. S. Logier has been writing about Canadian amphibians and reptiles since 1925 and must be considered the first outstanding contributor to Canadian herpetology. Although most of his publications pertain to Ontario, his interests have always been Canadian wide, and his years of gathering records have finally culminated in his 1955 "Check List of Amphibians and Reptiles of Canada and Alaska." This work contains the first spot distribution maps ever to be published for Canadian amphibians and reptiles. Each species is mapped, and the record source given for each spot on the maps. The list contains 36 of my own recent range records and is therefore more accurate on the eastern Canadian species than any previous reference.

My own paper on "Range Extensions of Amphibians in Eastern Canada" was published in 1954 in the Canadian Field-Naturalist and contains 51 records. It is in essence a summary of little known and new records for all of Eastern Canada north to the tree-line including the major islands of the Gulf of St. Lawrence. Fourteen species are discussed, and many of the ranges are hundreds of miles in extent.

Eastern Ontario

Eastern Ontario is defined as that part of the Province east of a line from Pembroke to Kingston. This region has a remarkably poor herpetofauna when compared with southwestern regions of the same province. Consequently, it was not so attractive to the early Ontario naturalists, who confined their collecting and remarks to the latter area. A publications outlet for nature observations by eastern Ontario naturalists was provided by the founding of the Ottawa Field-Naturalists' Club in 1879, and soon after herpetological notes were contributed. However, the first list of amphibians and reptiles for the region was not published until 1918. This list of 20 species from the Ottawa area by C. L. Patch has since been increased to 30 species. One of the additions was the Map Turtle *Graptemys geographica,* which was reported from the Ottawa River drainage for the first time by Patch in 1925.

In the same year, Dymond's annotated list of the amphibians and reptiles of Lake Abitibi appeared. It is an important contribution because the paucity of snakes and the absence of turtles in that area demonstrated that their northern limits lie somewhere to the south of this lake.

"The Amphibians of Ontario" by Logier (1937) is a descriptive pamphlet and mentions distribution only, generally for some of the rarer forms. However, his "Reptiles of Ontario," published in 1939, treats the distributional aspect in some detail by giving county localities, mileages from specific points, and even verbal reports by local inhabitants. Nevertheless, both handbooks are weak on eastern Ontario specifically, because they lack collections from this region.

Toner and St. Remy helped remedy this situation in 1941 with their "Amphibians of Eastern Ontario." They summarized the scattered published records—old unpublished collections in the Royal Ontario

Museum and National Museum of Canada—and added the results of their own field work to give a complete coverage of records for the eastern peninsula of Ontario to as far west as Frontenac and Renfrew counties.

Quebec

Perhaps the first herpetofaunal survey ever to be conducted in Canada was D'Urban's natural history survey of the Rouge River from May 13 to October 19, 1859. His party travelled the river from its junction with the Ottawa River near Calumet to its tributaries in the Lake Tremblant area and visited as well many tributary streams and lakes. His list is well annotated, and his remarks as to relative abundance and rarity of various species are most valuable, because little herpetological collecting has been done in this southern Laurentian region since that date.

The next major contributor in Quebec was Provancher, who founded the periodical "Le Naturaliste Canadien" in 1868, and in whose honour the Provancher Natural History Society was formed. He contributed articles on amphibians and reptiles from 1869 until 1878, and his two most important ones are "Faune Canadienne: Les Reptiles" in two parts, 1874 and 1875. These papers deal with the amphibians and reptiles of the St. Lawrence River Valley from Montreal to Quebec City. In addition, he mentions the earlier occurrence of the Milk Snake, *Lampropeltis doliata triangulum*, in the Eastern Townships and the absence of turtles in the Saguenay Valley region.

It was not until 1937 that anything was published again on Provancher's territory. In this year Alexandre produced "Les Couleuvres du Québec" and "Les Tortues du Québec," which, unfortunately, do not contain any distributional data. The same holds true for his 1945 treatment of Quebec frogs and toads. However, the locality records gathered by Alexandre were sent to Logier and have been incorporated in the latter's 1955 "Check List of Amphibians and Reptiles of Canada and Alaska." Many of Alexandre's collections constitute valuable range extensions.

During 1937 Trapido and Clausen collected amphibians and reptiles in Quebec from the Lake St. John area, along the south and north shores of the St. Lawrence River, in parts of the Eastern Townships, and in the Gaspé Peninsula. In 1939 they published their findings and performed a valuable service by reviewing the previous Quebec literature in their discussion of each species.

Another contribution to our knowledge of the Gaspé salientia was made in 1939 by Moore and Moore, who added three frog species to the Trapido and Clausen list and reported on the relative abundance of these and several other species.

The first and only annotated list of amphibians of the Laurentide Park was issued by V. D. Vladykov in 1949, but it is of a cursory nature with only collections of larvæ representing some of the species.

An inclusive popular treatment, in French, of the amphibians and reptiles of Quebec province was written by C. Melançon in 1950. It is primarily concerned with life-histories and folk-lore, and contains a minimum of distributional data.

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Ungava and Labrador

The first collections and reports of amphibians from the subarctic regions of Eastern Canada came with Packard's 1866 report of frogs from the northern Labrador coast. One of his records, *Rana septentrionalis* from Okak, had remained in doubt until substantiated by the 1955 collections of D. Oliver, of McGill University, from the same latitude (specimens now at the National Museum of Canada) and the report of the "Blue Dolphin" collections from the Lake Melville area by Backus in 1954.

In the latter paper, Backus discussed the few previous records of amphibians from Labrador and listed the many localities where the "Blue Dolphin" expedition collected the four different species of anurans that they found.

The first collection ever to have been made of frogs near the eastern Canadian tree-line was of *Rana sylvatica* taken in 1948 by two separate parties. Hildebrand published a detailed report in 1949 of his observations at Fort Chimo on adult Wood Frogs, eggs and tadpoles. Gabrielson and Wright caught one *R. sylvatica* across the river from Fort Chimo and mentioned this in their 1951 report on the birds of that area.

Anticosti and Newfoundland

The early reports of Verrill (1863), Maret (1867), and Schmidt (1904) on the herpetofauna of Anticosti Island and Newfoundland were reviewed by Johansen in his 1926 paper on the amphibians and reptiles of the larger islands of the Gulf of St. Lawrence (exclusive of Prince Edward Island and Cape Breton Island). Johansen visited Anticosti, Newfoundland, and the Magdalen Islands and found no representatives on the Magdalens but did note that frogs had been introduced to the first two islands and were thriving and spreading there.

One of the few notes on the marine turtles of Canada was contributed by Squires with his 1954 paper on marine turtle records from Newfoundland waters.

New Brunswick

The first naturalist to write about the amphibians and reptiles of New Brunswick was A. L. Adams whose additional travels through the adjacent New England States had acquainted him with many species common to eastern North America. In his "Field and Forest Rambles" (1875) he discusses the occurrence of many amphibians and reptiles in Maine and New Brunswick. It is a rather disturbing list because he mentions certain species that are now known to be common in New Brunswick as being absent at that time, and records several species which have never since been observed in this province.

The only other major contributor to our knowledge of the amphibians and reptiles of New Brunswick is P. Cox. In addition to his papers already mentioned on the Maritimes in general, he compiled a list in 1898 of New Brunswick amphibians. The list is nearly complete, but as with Adams' account, it has a few species that have never again been reported from this province.

Prince Edward Island

The early writings on the herpetofauna of Prince Edward Island by Mellish in 1876 and Bain in 1890 are very general and seem to be compounded of equal parts of observation, hearsay, and imagination. The first list of the Island herpetofauna was done by Hurst in 1944, but he was concerned solely with the amphibians. The list is incomplete and lacks distributional data.

Nova Scotia

Nova Scotia's herpetofauna was reviewed for the first time by Jones in 1865. His excellent article (14 pages) included all the observations and reports that he could muster, including several very dubious ones.

A discussion of Nova Scotian snakes was contributed by Gilpin in 1875. In it he gives distributional data, life-history notes, measurements of eggs, young, and adults, and types of habitats that the various species seem to prefer.

During the latter part of the nineteenth century, a collection of Nova Scotian amphibians and reptiles was accumulated at the Pictou Academy. McKay performed a valuable service by publishing a list of these specimens in 1896, for in 1932 fire consumed the entire collection and accession books. Two species represented in that collection, namely *Hyla v. versicolor* and *Coluber c. constrictor,* have not been preserved in any other Nova Scotia collections.

H. Piers, curator of the Nova Scotia Provincial Museum from 1899 to 1940, was a very careful observer and recorder, and annually reported on the provincial amphibians and reptiles that were acquired by the museum. Unfortunately, most of his records are buried in the "Annual Reports of the Provincial Museum and Science Library" and have received little attention. Until the past few years, he was the only Canadian herpetologist who had a keen interest in the marine turtles, and most of our records of these forms are the result of his efforts.

Not until 1952 was any further significant information published on the amphibians and reptiles of this province. In that year Richmond contributed a brief but valuable annotated list of nine amphibians and reptiles from poorly studied Cape Breton Island, and Bleakney published "The Amphibians and Reptiles of Nova Scotia." The latter consists of an annotated list of 22 species and subspecies, containing distributional data, measurements, spot and scale counts with discussion of same, notes on life-histories, and new information on the life-histories of several species, as well as a brief discussion of the effects of the post-glacial climate on the herpetofauna of Nova Scotia and New Brunswick.

If only the major papers on the distribution of the eastern Canadian herpetofauna are considered over the past hundred years, then the general sequence of this literature is one of three phases: a period from 1859 to 1907 of fifteen important papers with a peak of contributions in 1899; a hiatus from 1907 to 1926; and a total of fifteen papers since that date, with six of them contributed since 1950.

Few of these articles and notes give any idea of the relative abundance of individuals of the different species of amphibians and reptiles in one area, or the relative abundance of the same species in different areas. However, this writer found that population densities and species composition both vary considerably from region to region, often strikingly, and it is from a knowledge of these variations that the Herpetofaunal Sections of Eastern Canada, described for the first time in this paper, can be derived.

MATERIALS AND METHODS

Most of the specimens used for the distributional data and nearly all of those used in the taxonomic studies, not yet published, were collected by the author. Because present practice attaches taxonomic significance only to the population as a unit, large series of specimens were collected wherever possible. Approximately 6,000 specimens of 34 species were collected personally, of which 3,700 are adult specimens. These specimens are now deposited at the National Museum of Canada and the Nova Scotia Museum of Science.

Additional sources of material include the many donations of specimens that interested persons made directly to me and specimens or information from other institutions, among which are the Nova Scotia Museum of Science, the Royal Ontario Museum, the New Brunswick Museum, the Quebec Provincial Museum, the Museum of the Miramichi Natural History Society of New Brunswick, the Institute of Parasitology, and Cornell University.

The literature consulted during this study is listed in "References and in the "Bibliography of Distribution Reports".

Accounts transmitted verbally by local inhabitants, particularly young boys, was another vital source of information. My main purpose with these questions was *not* to determine how many species occurred in any one area, because few people are acquainted with the many secretive forms of amphibians and reptiles, but rather to determine only the abundance of turtles and the Garter Snake in different localities. These animals can be termed climatic indicators, for they are most common in warm valleys and often absent elsewhere. Excluding extreme eastern Ontario and extreme southern Quebec, the rest of Eastern Canada is ideally suited to this kind of questioning because the three species of turtle and the Garter Snake are conspicuous animals, being active diurnal forms as opposed to secretive and nocturnal forms, and if they occur in an area, the local inhabitants know of it. Where these reptiles are abundant, most other eastern Canadian amphibians and reptiles are also common, and, conversely, where they are scarce or absent, the herpetofauna is generally poor in species and individuals.

Specimens collected include eggs, young, and adults. Many of the amphibians were taken at night by the light of a five-cell battery headlamp, especially during the breeding season when they become concentrated at the egg-laying sites. The reptiles were collected for the most part during the daylight hours. Dip-nets, 6-foot and 15-foot sweep seines, snake tongs, and .22 and .410 caliber shot were employed in gathering specimens. Field notes on temperature, habitats, habits, and other observations were recorded. An effort was made to capture the specimens alive so that they could be killed later with ether and measured in a relaxed condition. The sex and various measurements were recorded directly on data sheets.

All specimens when etherized, measured, and labelled were injected with 5 per cent formalin and arranged in a fixing pan containing 5 per cent formalin. After a period of from 2 to 24 hours in the fixing bath, the amphibians were stored in 3 per cent formalin, the snakes in 5 per cent formalin, and the turtles in 10 per cent formalin. Specimens at the National Museum of Canada are stored in the dark at a constant temperature of 52° F.

DESCRIPTION OF AREA

The area from which specimens have been collected or examined by the author includes Newfoundland, Anticosti Island, Nova Scotia, Prince Edward Island, New Brunswick, Quebec, Labrador, and southeastern Ontario. The region is approximately 1,100 miles from east to west and 1,000 miles from north to south, an area equivalent to the entire United States west of the Mississippi River.

The physiography and climate of this vast region are varied and, as will be shown in a later discussion, exert a profound influence on the abundance and distribution of the poikilothermous herpetofauna. Map 2 indicates those areas which are over 1,000 feet in altitude. Broadly speaking, the area may be divided into a southeastern Appalachian element of a complex of intrusive, sedimentary, and volcanic rocks (Newfoundland, Nova Scotia, Prince Edward Island, New Brunswick, Gaspé, and extreme southeastern Quebec); a northern Canadian Shield element of Precambrian intrusive rocks (Quebec north of the Ottawa and St. Lawrence rivers, and Labrador); and a central and southwestern St. Lawrence Lowlands element of Ordovician sedimentary rocks (Anticosti Island, southern Quebec, and eastern Ontario); (Geological Survey of Canada, map 1045A, 1954). The entire region has been glaciated, and glacial deposits overlie much of the bed-rock formations. Because of this glaciation the present flora and fauna consist entirely of postglacial immigrants.

In spite of their maritime location, the Atlantic Provinces do not have a maritime climate (Climate of Canada, Department of Transport, Meteorological Division, 1949). This is due to the fact that the prevailing air masses which bathe this section of the country arrive from the west and carry with them the continental summer heat or winter cold. A true maritime climate is experienced only on the coastal islands and along coastal Newfoundland where the extremes of both summer and winter air temperatures are lessened by the cold Labrador Current from the arctic (*See* map 3 for Maximum summer / minimum winter mean monthly temperatures).

The western St. Lawrence Lowlands are subjected to invasions of dry polar air, warmed moist Pacific polar air, polar air returning from the south (and intermediate to the first two-mentioned air-mass types) and warm moist subtropical air. Alternation in air flow occurs about every three days, and rain usually accompanies the leading edge of the air masses, so that the region experiences a variety of temperatures and precipitations on short notice plus a continental climate of severe winters and hot summers.

A third climatic division can be referred to as the Laurentian Plateau. It includes most of Quebec and Labrador north of the Ottawa and St. Lawrence rivers. The southern boundary of the Plateau by its very altitude (upwards to over 3,000 feet) makes it cooler than the adjacent lowland river plains, and, in addition, summer outflows of polar air move across the cool waters of Hudson Bay and pour over this region. The clear skies that accompany these masses are conducive to night heat radiation by rocky ridges, which further cools the air and causes it to drain into lower levels. Consequently, frost is frequent except near large lakes and rivers. Moisture-laden air masses from the south usually precipitate upon contact with the plateau resulting in a maximum mean annual rainfall of 30 to 50 inches for Eastern Canada along the southern boundary of the plateau and a minimum mean annual rainfall in northern Ungava of 15 inches (Hare, 1950).

According to Thornthwaite's moisture classification (Sanderson, 1948), all of Eastern Canada falls within his humid division. Lack of moisture is therefore a negligible factor in limiting the distribution of amphibians and reptiles in Eastern Canada, except in far northern Quebec where moisture takes the form of soil permafrost and surface ice and snow.

Within recent history, forest covered most of this region, but along the southern boundary of the area, man has cleared many of the fertile valley slopes for purposes of cultivation, and the endless demand for lumber has further reduced the original forest cover. A broad classification of the forests of Eastern Canada is provided by Halliday (1937). He divides the area into three main formations: the southeastern Acadian Forest Region of Nova Scotia, Prince Edward Island, and New Brunswick with its mixture of conifers and broadleaf hardwoods; the Great Lakes – St. Lawrence Forest Region, also of conifers and broadleaf hardwoods but of different species; and the great Boreal Forest Region of the Gaspé, Quebec north of the St. Lawrence River, and Labrador, dominated by conifers.

The climate along the southern border of this eastern region of Canada is propitious to 21 species of amphibians and 22 of reptiles. North of the St. Lawrence River, the limiting factor of low temperature modifies the otherwise suitable habitats to the extent that only 11 amphibians and 3 reptiles are found along the southern margin of the Laurentian Shield, and at the tree-line in Ungava there exists scattered colonies of but 2 species of frog.

RARE OR QUESTIONABLE REPORTS

The extent to which the writer's collections have altered the previous distribution picture of amphibians and reptiles in Eastern Canada warrants a detailed summary of the distribution of nearly every species. However, since 43 species and subspecies are involved, it is felt that spot distribution maps will convey a more accurate and meaningful picture than a cumbersome verbal delineation of range and records for each species. Therefore, I have drawn northern range limit lines on these maps according to the recognized North American texts (Wright and Wright, 1949; Carr, 1952; Bishop, 1943; Schmidt and Davis, 1941; and Smith, 1946) and filled in with dots all the known locality records from both my own survey and those of previous workers. The records used in plotting these maps are on file at the National Museum of Canada.

The importance of using spot distribution maps for delimiting the periphery of a species range has been emphasized by Schmidt (1950, p. 9). He points out that the range limit usually is geographically irregular and may even consist of discontinuous populations. This is of the greatest importance to speciation. "Thus it is of the utmost importance to evolutionary studies to define the borders of the ranges of species and subspecies of animals . . . " and "as geographic limits of the species are important, individual locality records are important . . . Dr. E. R. Dunn and I (in litt.) have discussed the matter of the instructiveness of 'spot maps', coming to the mutual conclusion that the limits of supposed ranges shown on maps might well be supplemented by the actual spot records. . . ." A comparison of the published limit lines drawn on my maps with actual spot collecting localities serves as a dramatic illustration of which method is the more informative and accurate. Logier and Toner, 1955, have effectively employed the spot locality method for all of Canada and have shown that it is almost essential when working with poorly known peripheral populations.

In order to enhance the value of my distribution maps, I have used several kinds of spot symbols. Collections made and reported by others are represented by black circles. My own contributions are represented by black triangles and are made up of (1) localities where I personally caught the specimens, (2) collections made by others but donated directly to me, and (3) any previously unreported records that I have discovered. Questionable records are represented on the maps as black squares.

There are certain published and unpublished records that, because of insufficient data, their doubtful validity, or obvious incorrectness, deserve clarification. These will now be discussed, province by province.

Ontario

In a report of a field excursion to Hogsback, near Ottawa, Small and Lett, 1884, mentioned the "small semiaquatic salamander under stones at edge of rapids at Hogsback . . . probably the yellow desmognath *Desmognathus acrophaea*." Again from Hogsback, Latchford, 1827, says *Desmognathus fuscus* is abundant under stones. In actual fact, no specimens of this genus have been found within 130 miles of Ottawa, and I have collected at Hogsback on a number of occasions and found only *Eurycea bislineata bislineata,* which is common throughout this region.

Another dubious Ottawa record appears in Cope's 1889 "The Batrachia of North America." It is a United States National Museum specimen of "*Ambystoma tigrinum*" from "Ottawa, Canada." However, present-day evidence indicates that this large salamander occurs in Eastern Canada only at Point Pelee in southern Ontario, and is even rare there. Dunn (1904, p. 61) considers the Ottawa specimen of dubious provenance since it is of the western subspecies *diaboli.*

In the same publication, Cope has another questionable record which is a collection of three *Rana palustris* from "James Bay, New Brunswick" (Logier, 1955, wrongly attributes this record to Preble, 1902, who actually was quoting from Cope). Because there is no "James Bay" locality in New Brunswick and because the collector, C. Drexler, collected several other species of amphibians in the James Bay and Hudson Bay area, this record is considered to be valid for James Bay, even though the nearest collecting site for this frog lies 300 miles to the south. This record has always been viewed with scepticism, and unreasonably so, I feel, since no one has since searched for *R. palustris* between Lake Superior and James Bay.

There are two large specimens of *Elaphe vulpina gloydi* in the National Museum of Canada's collections labelled "Ottawa 1899" and "Prescott, Ontario, Sept. 18, 1926." Neither of these records have ever appeared in print, and the nearest additional reports are from Parry Sound, 190 miles to the west. It is interesting, however, that Edna Ross of the Ottawa Field-Naturalists' Club described to me what must have been this snake. She had seen it in early August 1954 at Pakenham, some 30 miles west of Ottawa.

There are two mounted adult *Amyda ferox spinifera* in the National Museum of Canada's collections, which have no data on them except that they came from the Blanche River near the Rockcliffe Rifle Range, just east of Ottawa. Judging from the catalogue number they were collected about 1900, and only a single specimen (Clark, 1908) has been taken from the Ottawa River drainage since that time. However, they are known from the St. Lawrence and Richelieu rivers, and I believe that if the proper collecting techniques were employed these old records would be substantiated.

Quebec

In 1931, at Natsitok, on the east coast of Ungava Bay, Hantzsch wrote that he saw very large tadpoles in the daytime and heard "several times short squeaking and trilling notes" at night but, unfortunately, was unable to collect any specimens. This report has since been quoted by Logier and Toner, 1955, and Bleakney, 1954. However, as reported in the latter paper, my own work along that coast indicated that *Rana sylvatica* might possibly be relict in the *upper* reaches of some of the valleys where large specimens of relict *Picea mariana, Larix laricina,* and *Betula papyrifera* have been found (Rousseau, 1951). Nevertheless, the occurrence of frogs and tadpoles along the barren exposed coast seems most unlikely, and as previously reported (Bleakney, 1954), the Eskimos camping along this coast claim that there are no frogs north of Fort Chimo and George River. I offer the following explanation of Hantzsch's observations. The "tadpoles" were probably the deservedly named Tadpole Shrimp, *Lepidurus arcticus* (order Notostrica), which frequent cold water and melt-water habitats. Since the call-notes of northern frogs are made mainly during the few days of the spring breeding season and Hantzsch heard noises on August 16, it is unlikely that any anuran was responsible. It is far more likely that birds, especially migrating species, were the source.

Logier and Toner, 1955, are the first authors to quote the 1878 "La Salamandre saumonée" reported by Provancher from Chicoutimi, east of Lake St. John in Quebec. Logier assigns the specimen to *Plethodon c. cinereus*, but I think *Eurycea b. bislineata* is correct. Provancher's colour description of the yellowish brown dorsum and the salmon yellow ventrum does not fit *P. cinereus* but is accurate for *E. bislineata*. However, the size of 5 inches is about one inch in excess for both species. Logier himself in 1952 said that *P.c. cinereus* rarely exceeds 4 inches in length. The 5-inch measurement may have been an estimate, in which case it would probably be excessive.

In Logier and Toner's 1955 "Check List of Amphibians and Reptiles of Canada and Alaska" they quote Provancher (1874) as saying that *Clemmys guttata* occurs at Nicolet and Quebec City. This is a mistranslation of the original French text which claimed this species to be very rare, known only from Nicolet and not to be expected at Quebec City. No specimens have been reported since Provancher's time, but I do not believe anyone has searched for them. There may well be a relict population at Lake St. Peter.

Labrador

The report in my 1954 paper of *Hyla c. crucifer* from Menihek Lake, which is some 300 miles north of any previous records, was from a verbal one given to me in 1952. It will have to remain unconfirmed until specimens are collected. Nevertheless, a look at Logier and Toner's 1955 distribution map of this species shows a similar situation in the west where specimens were collected at Great Slave Lake, which is over 900 miles from the nearest records. Obviously the distribution of *Hyla c. crucifer* is poorly understood.

During the summer of 1955, Mr. W. J. Smith collected for the National Museum of Canada in the Lake Melville area. The local occurrence of a small salamander was mentioned to him on several occasions, and from the descriptions it must be *Plethodon c. cinereus*. One specimen of *Ambystoma jeffersonianum* constitutes the only other salamander report from Labrador.

Backus in his 1954 notes on the anurans of Labrador incorrectly credits Packard, 1866, with reporting *Rana sylvatica* from Okak. The specimen was *Rana septentrionalis* as identified by Cope, and simply because it was much farther north than any previous reports, the fashion has been to ignore it, as have Wright and Wright in their frogs of North America (1949), and Moore in his study of this species (1952), or to correct it as Backus has attempted to do. Recent collections have proved that Packard's report is not at all unreasonable.

Anticosti Island and Newfoundland

Both Wright and Wright in the 1949 "Handbook of Frogs and Toads" and Logier in his 1952 "Frogs, Toads, and Salamanders of Eastern Canada" are incorrect concerning the distributions of *Rana p. pipiens* and *Rana clamitans* on these two islands. Logier has since corrected himself in his 1955 "Check List of Amphibians and Reptiles of Canada and Alaska." Backus, 1954, criticized Wright and Wright for not explaining that these *two* species were introduced into Newfoundland, and thereby himself blundered, for only one species, *Rana clamitans*, is known from Newfoundland. It is difficult to fathom why these mistakes should persist, for Johansen in 1926 correctly discussed the herpetofauna of these two islands in detail. I have examined his original specimens which are at the National Museum of Canada.

New Brunswick

There are quite a number of amphibians and reptiles listed in Adams' 1873 account of New Brunswick's fauna that have not been reported since that time. Assuming that his observations are correct, his report of one Spotted Turtle, *Clemmys guttata*, and many Musk Turtles, *Sternotherus odoratus*, are not impossible because both species are known from southwestern Maine and thus could exist as relict populations in New Brunswick. However, it is peculiar that they have not since been found because turtles are conspicuous animals.

Adams also described the Milk Snake, *Lampropeltis doliata triangulum*, but does not say how common it was. I have heard of no further reports.

The validity of his report of the Blue-tailed Skink, *Eumeces fasciatus*, is extremely doubtful; first, because it is a very conspicuous animal and, peculiarly enough, abundant wherever it does occur, even in the north, and secondly, because its known northern limit on the eastern side of the Appalachians is in Massachussetts, 400 miles to the south.

In spite of these unusual records, Adams overlooked some of the common species. He says that the Black Snake (*Coluber c. constrictor*), Red-bellied Snake (*Storeria occipitomaculata*), and Ring-necked Snake (*Diadophis punctatus edwardsi*) were known from Maine but not yet from New Brunswick. I have had one Black Snake described to me at Grand Lake, N. B., and the other two species are common throughout the Maritimes. In another instance he describes an "unknown species of salamander," which is obviously the common Jefferson's Salamander, (*Ambystoma jeffersonianum*).

Cox in his 1898 Batrachia of New Brunswick was correct when he said that the Common Tree Frog, *Hyla v. versicolor,* is rare in that province. However, its exact distribution is somewhat of a mystery, for he claims to have heard its call (a very distinctive one) "in several parts of the province," but the only specimen he ever saw was one from Gloucester County in the Miramichi Natural History Association Museum at Chatham. I visited this museum in 1955 and found many of the original specimens collected by Cox, but no specimens of *Hyla v. versicolor*. Since the time of Cox the species has been recorded only from the Fredericton area, which is 100 miles south of Gloucester County. I have searched for this tree frog in New Brunswick during two of its breeding seasons (1953 and 1955) but have heard and captured it only near Fredericton.

In the same paper by Cox and in his 1907 "Lizards and Salamanders of Canada" he mentions *Plethodon glutinosus* as being extremely rare in the southern parts of the province. He makes no reference to personal experience with the species. That he should mention it at all is unusual because its northern limit is in southern New York State. The report could be based on hearsay from someone who confused an *Ambystoma jeffersonianum* with *Plethodon glutinosus,* a common mistake.

Another dubious report by Cox in 1907 is that of *Desmognathus ochrophaeus* from the St. John River Valley, as identified by Cope. Dunn examined the two specimens and found them to be *D. f. fuscus* (Dunn, 1926, p. 93). This is in keeping with the known distribution of these two species.

Prince Edward Island

Rana palustris has been listed from this island by Cox (1899) and Hurst (1944), and although no specimens are available to confirm this, the paucity of collecting done on the island makes it impossible to deny their statements. The same holds true for Fowler's 1915 report of *R. septentrionalis* from several localities on Prince Edward Island.

Nova Scotia

Undoubtedly the most remarkable report from Eastern Canada is Jones' 1868 *Hyla squirella* from Nova Scotia. This species occurs in the southeastern United States and could have reached Nova Scotia only if it had been imported. In any case Jones failed to give a description of the specimen, and of the locality and circumstances in which it was collected.

The validity of another of Jones' Nova Scotia records, *Hyla v. versicolor* (1865), is questionable, to say the least. I quote it in full. "There are no specimens, but an Indian told Captain Hardy that he saw one in the crotch of a maple tree." The only other reference to the species occurring in Nova Scotia is in McKay's 1896 paper where he includes it in his list of native species in the Pictou Academy collections. I have searched diligently for this species in the province but without success.

This writer firmly believes that Blanding's Turtle, *Emys blandingi,* is a native Nova Scotian species, but the evidence is so scanty that a complete review is warranted. The nearest collecting records to Nova Scotia are in southern New Hampshire State and eastern Ontario. On June 8, 1953, I caught a large female of this species in Lake Kejimkujik, Queens County. This was the first evidence that this turtle occurred in the Maritimes. It had "1952" on the plastron and only after three years of inquiry did I locate the persons who had carved the date. They had found the animal laying eggs on the beach at their cottage, and recognizing it as different from the common Painted and Snapping Turtles of the lake, they had carved the date and released it. Their capture and mine were both made within 100 yards of one another, and this and the fact that the turtle was laying eggs, and had, as the carved date proves, survived for a full year, led me to believe that it was not an escaped pet but rather a representative of a relict population of *Emys blandingi* in Nova Scotia. This suspicion was substantiated in early July, 1955, when I received a verbal report of two more specimens from the same part of the lake. Mr. Baxter, director of the Dominion Fish Hatchery at Lake Kejimkujik and a very keen observer of the local fauna, told me that during the last week of June many turtles were crawling across the hatchery property to lay eggs in the gravel-bank behind his home, as they do annually. He said that in addition to the Painted and Snapping Turtles, he had picked up (and to my sorrow subsequently released) two specimens of a turtle he had never seen before. His description of the high box-like shells and the "sulking" behaviour of the one he released in the lake, in contrast to the frantic fleeing behaviour that the Painted and Snapping Turtles invariably exhibit when released, is irrefutable evidence of *Emys blandingi* in Nova Scotia. As undoubtedly these two were females seeking egg-laying sites, there must have existed a breeding population.

Maritime Provinces

The depicted ranges on the distribution maps of *Rana catesbeiana* and *Chrysemys p. picta* by Wright and Wright (1949) and by Carr (1952), respectively, far exceed the actual range of these species. These authors have included northern New Brunswick, Gaspé Peninsula, and too much of southern Quebec in their maps, despite the absence of any records from the areas. However, in the text Wright and Wright describe the range of *R. catesbeiana* in Canada as "Lake Huron to Maine," which is south of the true northern limits of this species, and far south of the line on their map. Similarly, Carr's written description of the northern limit of *Chrysemys p. picta* is south of the lines on his own map.

There is one species that deserves special mention, and it involves New Brunswick, Prince Edward Island, and Nova Scotia. It is *Coluber c. constrictor*, a glossy black snake that reaches 4 to 5 feet in length. There is no other maritime snake that could be confused with it. It has been reported from Nova Scotia and Prince Edward Island by several of the early writers (Gilpin, 1875; McKay, 1896; Piers, 1890; and Mellish, 1876). I myself have heard black snake stories in Nova Scotia, Prince Edward Island, and New Brunswick, yet there is not a specimen in existence that can be credited to Canada. There is, however, one adult specimen in the Nova Scotia Museum of Science which was found by Piers in an unlabelled bottle among the museum's collections. The history of this specimen is an enigma.

The case of *Natrix s. sipedon* in maritime Canada is in a somewhat different category, for it has never been entered on any lists of the area, nor has a specimen been caught. However, the term "water snake" is often used by local inhabitants. From my personal experience in these provinces I do not believe that any water snakes exist in maritime Canada. All such reports pertain to the Garter Snake, *Thamnophis s. sirtalis*. The fact that Garter Snakes often live in the vicinity of water and readily take to it if disturbed is possibly one reason for these reports. A second reason may be due to the fact that the maritime Garter Snakes are brownish (with varying degrees of yellowish brown or greenish brown) and often have no stripes or only poorly developed stripes, details which are in sharp contrast to the usual striped form with its three light or bright yellow stripes. This brown stripeless form of *T. s. sirtalis* is easily mistaken for *N. s. sipedon* by those who are familiar with the latter snake in central Canada or eastern United States. I have certainly found no convincing evidence that *N. s. sipedon* occurs in the Maritime Provinces. However, its abundance locally at Bangor, Maine, raises the possibility of there being relict populations in New Brunswick, but all evidence indicates that if relict in New Brunswick, it would be centred at Grand Lake, and such is not the case.

The three species of marine turtles recorded from Eastern Canada do not breed there, but a few individuals are usually reported annually by fishermen who have seen or caught them in their nets. There have been a few reports of *Dermochelys coriacea coriacea*, only two records of *Caretta caretta caretta* (Squires, 1954; and a painting at the National Museum of Canada of a specimen taken off Halifax on August 20, 1931), and four records of *Lepidochelys olivacea kempi*. The latter were correctly identified by Bleakney, 1955, from old "*Caretta caretta*" specimens in the Nova Scotia Museum of Science and the National Museum of Canada.

ZOOGEOGRAPHY

Eastern Canada is a peripheral region as regards the ranges of all the amphibian and reptile species that occur there. These ranges reach their northern limit somewhere within its boundaries, and as the environmental factors approach the specific limiting value, two phenomena are evident. One is that the northern limit line of many species, although in general oriented east and west, possesses northward projecting peninsulas and even outlying islands. The second observation is that along the periphery of a species range, its population density varies strikingly. This variation is in contrast to its uniformity further south where the environment is propitious throughout.

The latter phenomenon is a reflection of the present-day environment. The first phenomenon is a reflection of the history of the environment since early postglacial times to the present and will be dealt with after the present-day picture has been clarified.

Present-day Herpetofauna

This existing situation of varying population densities and varying species composition within the herpetofauna of Eastern Canada has not previously been recognized or analysed. Because this pattern of variations in population densities was naturally not recognized until after much of the area had been surveyed, and because it was then too late to attempt an objective determination of species population densities, I have had to rely on a subjective analysis using the three descriptive terms—*abundant, common,* and *rare.* I feel, nevertheless, that these terms are meaningful, especially to students who have worked with vertebrate animal populations in the field. Tables 1 and 2 are a summary of this herpetofaunal information. In cases where I have insufficient data to voice a reasonable opinion a question mark (?) appears in the tables.

Without doubt the best index or indication of the suitability of an environment is the flora and fauna which live there. Therefore I propose to utilize the forest cover pattern of the region as background for the herpetofaunal zoogeographic pattern. The two coincide admirably, which is to be expected because both flora and herpetofauna are functions of the same variables. The distribution of the tree species in northeastern North America follows the temperature isotherms rather closely (Halliday 1950). Every organism has a narrow range of temperature within which it functions most effectively, and those animals such as the poikilothermous amphibians and reptiles, whose body temperature is determined (or at least limited) primarily by the external environmental temperature, have a distribution pattern that is profoundly influenced by environmental temperatures which are lower or higher than the optimum range for the species. As to the forest cover, it is well known (Oosting, 1949) that tree species occurring on both north- and south-facing slopes of the same mountain will reach a higher altitude on the south-facing slope (in the northern hemisphere) because of the greater amount of insolation received. Again, trees at the arctic tree-line have northward-extending tongues up the deep sheltered valley, as is admirably shown on Halliday's map of Forest Classification of Canada (1937), and by Munns' maps of tree species (1938). Map 4 in this paper is based on Halliday and modified by me, but in addition the following references were consulted on forest classification: Hare, 1950; Hustich, 1949; Roland, 1945; Rousseau, 1948; Nichols, 1935; and Villeneuve, 1946. These authors agree on the major picture and on the species distribution but not on the minutiæ of forest classification. Their arguments are in the realm of the botanist and will not be reviewed here. In addition, I feel it unnecessary to cite the forest components of each section, as this is admirably treated by the above authors; only the recognition of the existence of a south to north forest sequence and vagaries of distribution is relative here. Halliday's three major divisions of (1) Great Lakes – St. Lawrence Forest Region and (2) Acadian Forest Region merging into (3) a single Boreal Forest Region are employed for simplification and clarity. However, I must point out that neither Halliday nor the others have emphasized a most significant and obvious phytogeographic formation characteristic of the Maritimes, i.e. the narrow coastal belt of Balsam Fir and Red Spruce, both boreal forest elements. I therefore correct Halliday's 1937 map as follows (represented by dotted line on Map 4):

(1) In New Brunswick on the Bay of Fundy shore there is a coastal belt of fir and spruce conifers along the mountains. Halliday has shown the broadleaf trees of the lower St. John River Valley as extending right down to the sea-coast. It is interesting to note that the United States Department of Agriculture in Miscellaneous Publication No. 287 (Munns, 1938) has mapped the following deciduous trees as occurring in eastern maritime Canada but not found along the coasts: American Elm, Pin Cherry, Choke Cherry, Silver Maple, White Ash, Hophornbeam, Grey Birch, Paper Birch, and Red Oak.

(2) A horseshoe-shaped coastal belt of Balsam Fir and Red Spruce exists around the west, south, and east shores of Nova Scotia. Inland from this is an excellent forest of pines, Hemlock, and northern hardwoods. Halliday hints at this in his 1943 paper but does not pursue the point. His map of population intensity of Balsam Fir shows that in all of maritime Canada only a pocket in south-central Nova Scotia has less than 10 per cent, whereas much of the coast has over 30 per cent intensity. Again, his map for spruce shows a horseshoe coastal belt around southern Nova Scotia of 60 per cent and up, for population intensity. This high percentage is found again only on the Shickshock Mountains of the Gaspé and in Quebec and Labrador north of Latitude 50°N. This is a very important feature of the province, for it shows that the coasts are, environmentally speaking, more northern than is the inland habitat. In this connection, Ferguson (1952–53) says that several species of Lepidoptera in eastern North America, which occur in northern Quebec, Labrador, and high in the Appalachian Mountains, are found again in the cold sphagnum bogs and along the exposed sea-coasts of Nova Scotia.

It is assumed that each species of amphibian and reptile has its preferred or optimal temperature range, which differs (usually) from every other species, and on this account we find the various amphibian and reptile species in Eastern Canada reaching their northern limits at different latitudes. Moore (1939, 1940, 1942) has demonstrated a correlation between the lower limiting temperature for development of eggs of four species of *Rana* (which means the temperature at which the species begins to breed and lay), as determined in the laboratory, and the geographic distribution of these species of eastern North American frogs. He found that *Rana sylvatica*, which lays in the early spring of the year in water at or slightly above 2.5°C. develops normally at those cold temperatures and is the only species to reach the tree-line in Eastern Canada (near Latitude 58° N.) In contrast, the species *Rana catesbeiana*, which lays only during the heat of early summer in water at or above 15°C., reaches its northern limit along the St. Lawrence River Valley near Latitude 47° N. It is interesting to note that in this peripheral region all amphibians and reptiles spend from 5 to 8 months of each year in a state of hibernation.

In this region of Canada, there is not dearth of food, suitable cover, or moisture for amphibians and reptiles south of the arctic tree-line. Temperature is the predominant limiting factor (*See* discussion on Factors Limiting Distribution for further detail). As the climate becomes cooler toward the north, the suitability of the available environments is lessened, especially for those species whose optimum temperature falls outside the environmental temperature range, and a species becomes less and less abundant in the same type of habitat in different areas. To illustrate, the Painted Turtle, *Chrysemys picta* spp. is a typical example. In the vicinity of Ottawa this species can be seen in all of the rivers and lakes, and in most of the ponds. The same is true of south-central Nova Scotia where the ponds, streams, lake shores, and even roadside ditches have populations of Painted Turtles. I classify this type of occurrence as *abundant*, i.e. many individuals occupying every available suitable habitat. There is no trouble in locating the species in such an area. Now, north of Ottawa in the Gatineau Hills and in the Annapolis Valley of Nova Scotia, Painted Turtles occur but are found in only a limited number of situations. Their populations are confined to wind-protected ponds and those portions of lakes or rivers which have a lush growth of aquatic flora composed of such plants as *Nuphar, Nymphaea*, and *Potomogeton*. Such sheltered spots are warmer than ponds in the open or the open shore line of a lake where the wind blows away any warmed air and causes evaporation and cooling. Also the vegetation, both dead and alive, associated with weed beds retains solar heat better than a clear-water section of the shore line; decomposition of vegetable matter also produces some heat. I classify this type of occurrence as *common*, i.e., occurring in an area but with the populations limited to a few specific habitats. Some effort has to be made to locate specimens. In northern Nova Scotia and central New Brunswick this turtle is even more limited, for pond after pond, lake after lake (seemingly identical floristically and topographically with others in Nova Scotia and New Brunswick) were searched, but only the most protected warm pockets of certain lakes and forest-bordered ponds yielded evidence of the species. I classify this type of occurrence as *rare*, i.e. occurring in an area but limited to a very few samples of a common habitat. There is great difficulty in locating and collecting specimens in such areas, and the guidance of local long-time residents is usually essential. I have treated all of the eastern Canadian amphibians and reptiles in this manner and arranged the resulting information in Tables 1 and 2.

In summary, near the northern limit of a species range any section or pocket of the environment which is warmer than the adjacent terrain, usually at the microclimatic level, is a potential site of survival for poikilothermous amphibians and reptiles and may be the factor that permits the species to survive at that latitude in that particular region.

I shall begin my discussion of the present-day distribution of the eastern Canadian herpetofauna in Ontario, the area which has the most species, and progress eastward to the Maritime Provinces and thence northward into Ungava which has the smallest number of species. The different Herpetofaunal Sections described and referred to in this discussion are delineated and numbered on Map 5. The numbers indicate faunal relationships: Section 1 has the most species and Section 7 the least; numbers 2 and 2A have similar herpetofaunas and so with the other "A" numbers; and the islands have numbers preceded by "D" which means the fauna was derived from the corresponding mainland herpetofauna.

(a) *Eastern Ontario and Southern Quebec*

For the purpose of this study, eastern Ontario is defined as that part of the province between the Ottawa and the St. Lawrence rivers, east of a line drawn from Pembroke south to Kingston. The climate is continental with a mean July temperature of 70°F. and a mean January temperature of 12°F. and its southern border has the warmest summer weather of the entire study area.

Along the western boundary of the region is a narrow band of Precambrian granites and sedimentaries, and the rest of the area is mainly Ordovician limestone and other sedimentaries. The whole is drained by many small rivers into the Ottawa and St. Lawrence rivers. The Precambrian band is profusely dotted with lakes and bogs, whereas the Ordovician section is nearly lakeless and many of its streams become dry, or nearly so, in summer. The forest cover belongs to the Great Lakes – St. Lawrence Forest Region (Halliday, 1937), which is composed of an admixture of both conifers and broadleaf trees. Much of the original forest, however, has been heavily lumbered and cleared for purposes of cultivation.

Eastern Ontario has more species, 17 reptiles and 18 amphibians, than any other section of Eastern Canada. Most of the species are common, and several are abundant, particularly *Thamnophis s. sirtalis*, *Natrix s. sipedon*, and *Chrysemys picta marginata*. The forested lake region of the Precambrian formation, however, marks the northern and eastern limit of four species of reptiles, namely *Eumeces fasciatus*, *Elaphe o. obsoleta*, *Thamnophis s. sauritus*, and *Sternotherus odoratus*. I have used the northern limit of these four southern Ontario species for defining the boundary of Herpetofaunal Section 1 as shown on Map 5.

Excluding Section 1, the physiographic picture is one of the lowlands of the Ottawa Valley and extreme eastern Ontario merging into the broad St. Lawrence River Lowlands, which extend northeastward between the mountainous Precambrian Canadian Shield to the north and the Appalachian Mountains to the south. The tree species and the herpetofaunal elements extend northward via these lowlands and the valleys of tributary rivers, such as the Gatineau, St. Maurice, and Saguenay. The climate here is continental but with colder winters and cooler summers than in Section 1 (Map 3). Though lakes are few, numerous bays, inlets, and ponds occur along the courses of the Ottawa, St. Lawrence, and Richelieu rivers, and the thermal buffering action of these waters contributes to making the lowlands a warmer area than the mountainous country to the north and south. Much of it has been cleared for cultivation, but the original forest cover was of Great Lakes – St. Lawrence Forest species. In the foothills of the Laurentian and Appalachian Mountains the boreal forest elements of Balsam Fir and spruce are found at higher altitudes and merge into the White Pine – Hemlock – northern hardwoods (Nichols' 1935 forest equivalent of Halliday's Great Lakes – St. Lawrence Forest Formation) of the lower levels.

There are many species of amphibians and reptiles which have penetrated into these lowlands and foothills but cannot surmount the temperature barrier imposed by the latitude of the lower St. Lawrence Valley and the altitude of the mountains. The ranges of these species define the limits of Herpetofaunal Section 2 as drawn on Map 5. This assemblage of species consists of three turtles, *Emys blandingi, Graptemys geographica,* and *Trionyx ferox spinifera;* three snakes, *Storeria d. dekayi, Natrix s. sipedon,* and *Lampropeltis doliata triangulum;* and three amphibians, *Gyrinophilus p. porphyriticus, Hyla v. versicolor,* and *Pseudacris nigrita triseriata.* Within the shelter of the Gatineau Valley *Chrysemys picta marginata, N. s. sipedon, L. doliata triangulum,* and *H. v. versicolor* have managed to extend their range 100 miles farther north than in the adjacent terrain. The Gatineau Valley is also the only site where *P. nigrita triseriata* has crossed to the north side of either the Ottawa or St. Lawrence rivers and is found 20 miles up the valley at Wakefield. *G. p. porphyriticus* is common in the mountains of southern Quebec east of the St. Lawrence, but one specimen recorded from Ottawa (and of doubtful provenance) is the only record west of the St. Lawrence River. The southeast mountainous region of Quebec is the most southerly mountain-stream environment in Eastern Canada available to the Appalachian plethodont salamanders and it is here that *G. porphyriticus, Desmognathus f. fuscus,* and *Eurycea b. bislineata* have their highest population densities in Canada.

(b) *Lower St. Lawrence River Valley*

North of Herpetofaunal Section 2 to just past Quebec City the St. Lawrence River Valley narrows, the river begins to widen, and the climate becomes much cooler (Compare Montreal and Quebec temperatures on Map 3). The forest consists of the Great Lakes – St. Lawrence Forest Region species with increasing amounts of northern Boreal Forest species such as Balsam Fir and White Spruce. A climatic tongue penetrates nearly 100 miles up the valley of the St. Maurice River to the southwest of the 3,000-foot-high Laurentide Park mountains. The mean temperature at La Tuque, in the St. Maurice Valley, of 9°F. for January and 69°F. for July, is milder in summer than Quebec City with a January 10.7°F. and a July 66.7°F. Unfortunately, the St. Maurice Valley has had no herpetological attention whatsoever, but climatic and floristic evidence indicate that the situation is relative to the Gatineau Valley of Herpetofaunal Section 2 and that many species not occurring in the adjacent highlands should be found there.

Within this northern region of the St. Lawrence Lowlands the remaining turtles and all but one of the snakes reach an environment that is unpropitious for their existence. Herpetofaunal Section 3 as drawn on Map 5 shows the limits of their ranges with the St. Maurice Valley included on purely hypothetical grounds. Reaching their distributional limits here are the turtles *Chrysemys picta marginata, Clemmys insculpta,* and *Chelydra s. serpentina*; the snakes *Opheodrys v. vernalis, Diadophis punctatus edwardsi,* and *Storeria o. occipitomaculata;* and the amphibians *Rana catesbeiana, Necturus m. maculosus,* and *Desmognathus f. fuscus.* The latter species is found only along the streams of the Appalachian Mountains, and not on the west side of the St. Lawrence River. The turtle *C. p. marginata* and the salamander *N. m. maculorum* seem to be limited to the immediate vicinity of the St. Lawrence River and Lake St. Peter (as well as the Ottawa and Richelieu rivers of the previous Section); whereas *C. insculpta* and *G. s. serpentina* are rather rare but occur throughout Section 3.

(c) *Lake St. John and the Saguenay Valley*

About 100 miles north of Section 3 lies a flooded depression in the Precambrian Shield called Lake St. John. This large lake drains through a relatively narrow fault line as the Saguenay River into the St. Lawrence River. There is some Ordovician limestone in this basin (related to the limestones of the St. Lawrence Lowlands), but what is more important are the deep deposits of Pleistocene marine clays around the lake. This flat well-drained soil is readily heated by insolation, and the waters of the lake act thermostatically to help create a warm pocket in this region of the Precambrian Shield. As Halliday has shown (1937), most of the trees in this area are Great Lakes – St. Lawrence Forest species in contrast to the Boreal Forest species of the surrounding highlands. The Basswood tree, *Tilla americana,* is isolated here by 100 miles from the main body of the species' range to the south. There may yet be discovered similar examples of outliers in the animal kingdom with the advent of detailed studies of the fauna of the area. The available information on the amphibians and reptiles of this area is most inadequate. I have collected there only in early spring and thus have not obtained any other species than those of the cold water breeders which all range much farther north. However, judging from the available records of *Diemictylus v. viridescens, Ambystoma maculatum,* and *Rana palustris,* these species probably reach their northern limit within Herpetofaunal Section 4 as outlined on Map 5.

(d) *Nova Scotia*

Turning now to the maritime regions of Eastern Canada, a more complex zoogeographic picture is encountered, for there is considerable local climatic variation because of the complex physiographic structure of valleys and highlands and the peninsular and insular nature of much of this region. Five herpetofaunal islands, or pockets, where the abundance of species and individuals is greater than in the immediately adjacent areas, are recognized in this region with four of them in Nova Scotia.

The most southerly in latitude and the warmest region in eastern maritime Canada is located in the southwestern bulb of the Nova Scotia peninsula. The area is low relief, 500 feet high in the northwest, and slopes gently into the Atlantic Ocean in the southeast. It is composed of granites, slates, and quartzites. Because of the low altitude, cold sea air masses and coastal fogs sweep inland and affect the climate to the extent that a horseshoe belt of boreal fir and spruce trees extends along the west, south, and east coasts (Map 4). It is inland from this coastal belt that the magnificent forests of White Pine, Hemlock, and northern hardwoods exist—the same species that make up the Great Lakes – St. Lawrence Forest Formation. The numerous bogs and streams and particularly the large lakes in this area, such as Lake Rossignol (16 by 10 miles wide), Lake Kejimkujik (6 by 3 miles wide), Ponhook Lake (6 by 10 miles wide), and Malaga Lake (6 by 2 miles wide), are all important thermal buffers which help prevent the temperature from dropping excessively at night—a very important factor to amphibians breeding at night and to the incubation of buried reptile eggs.

It is within this latter central region, and not along the coast, that the greatest number of species and highest population densities are to be found in maritime Canada (*See* Tables 1 and 2). As can be seen on Map 6 the reptiles are more limited by temperature than the amphibians, and south-central Nova Scotia is unique in maritime Canada for its abundance of reptile species and individuals. This Herpetofaunal Section is designated as 2A, since it is the only area east of Herpetofaunal Section 2 in Ontario where *Thamnophis s. sauritus* and *Emys blandingi* occur and the only area in maritime Canada where *Chelydra s. serpentina, Chrysemys p. picta, Thamnophis s. sirtalis,* and *Rana catesbeiana* are abundant. It is also the only maritime region where the other three maritime snake genera, *Opheodrys, Diedophis,* and *Storeria,* are common.

It is unfortunate that meteorological data are not available as supporting evidence for the climatic uniqueness of this area in maritime Canada. The weather stations in Nova Scotia are only along the coast in this part of the province. However, in addition to the contrast of the forest cover at the coast and inland, there is further floristic evidence, for Roland says (1944–45, p. 22) that southwestern Nova Scotia has "at least 75 species [of plants that] are either confined to this area of the province or are else abundant here with only scattered stations elsewhere." He further states that 15 of these plants are found nowhere else in the Canadian maritimes but do occur again from Maine or Massachusetts southward.

A similar but mammalian example is the White-footed Mouse, *Peromyscus leucopus noveboracensis* (Dice, 1939), which occurs as far east and north as southern New Hampshire and then is found again in southwestern Nova Scotia and the nearby Annapolis Valley. Smith (1939) considers the Nova Scotian population and endemic race, *P. l. caudatus.* There is another mammalian feature which is peculiar to the area and that is the abundance of chipmunks, *Tamias striatus.* The area is teeming with them as I have witnessed in 1950, 1953, and 1955. Rand reported on the mammals of this region in 1933 and noted that "The Chipmunk is fairly common on hardwood hills, on the barrens and about clearings," in other words nearly everywhere. Sheldon spent summers in the area from 1919 to 1933, and she too was impressed, for in 1936 she wrote "Chipmunks are very common everywhere . . . . Chipmunk holes are everywhere." They occur throughout the rest of maritime Canada north to about Latitude 52°N., but A. W. Cameron (mammalogist at the National Museum of Canada) informs me that this is the only eastern area he knows of that has a high population density of this species.

Northeast of Section 2A the peninsula of Nova Scotia gradually constricts until it reaches a minimum width at the level of Windsor, Hants County. Because of the more northerly location and the proximity to the cold Minas Basin on the one side and the Atlantic fogs on the other, the rich herpetofauna of the southwest is severely depleted, except for certain elements that find the climate of the Annapolis Valley and the Windsor area of the upper Avon Valley propitious. Although the Annapolis Valley is on the northwest coast of the peninsula, it is considerably warmer than the adjacent terrain because it has the 500-foot-high South Mountain ridge and the entire eastern slope of Nova Scotia between it and the Atlantic Ocean to the south, and the 800-foot-high ridge of the North Mountain protecting it on the northwest from the cold air and fogs of the Bay of Fundy. The Bay of Fundy side of the North Mountain supports a fir and spruce forest (stunted in many areas) while the Annapolis Valley side has much beech, oak, and maple. The valley bottom has been extensively cleared for farming, but there is still evidence of excellent Red Pine, White Pine, and Hemlock stands, and oaks, Sugar Maple, Beech, and Yellow Birch. There is a good development of American Elm (*Elmus americana*), and Blue Oak (*Quercus bicolor*) has a disjunct population here, the next nearest localities being in southwest Maine. The mildness of the valley climate is evident in its excellent apple, pear, cherry, and peach orchards, for in spite of equally good soils in other parts of eastern maritime Canada no such crops can be successfully grown on such a large scale. The valley is of Triassic sandstone. It is 85 miles long and varies from 3 to 8 miles in width. It is characterized by a paucity of lakes which in warm summer days results in an interesting phenomenon. As the day progresses the hot humid air rises from the numerous lakes and bogs in the country to the south of the valley and forms into numerous cumulus clouds toward midday. This increases in the afternoon to form an intermittent cloud cover, whereas the sky over the lakeless valley remains clear and any clouds that drift over it from the adjacent areas become dissipated. This cloudless character undoubtedly accounts for the valley having a maritime high of 54 per cent bright sunshine in August. Putnam (1940, p. 141) states that "With the exception of the Annapolis Valley, nearly all of Nova Scotia has over 60% cloudiness, rising to 75% at the eastern end of Cape Breton Island."

As can be seen from Tables 1 and 2, the composition of the herpetofauna shows considerable change when compared with that of south-central Nova Scotia. *C. s. serpentina* is rare; *T. s. sirtalis, Storeria o. occipitomaculata, C. p. picta,* and *Rana catesbeiana* are only common, and none of the other snakes are common. This is not due to lack of suitable aquatic habitats, for the lakes along North Mountain and South Mountain are apparently identical in character to those in southwest Nova Scotia, and along the streams in the valley are many ponds, but only the more sheltered portions of these habitats are occupied. The only records of *C. s. serpentina* outside of this section are one specimen the author caught in southern Antigonish County; a specimen taken by H. White in West River, St. Mary's, Guysborough County; a verbal report from Oxford, Cumberland County; and a sight record on the sea beach at Port Hood, Cape Breton Island (the last by A. W. Cameron in 1953). The Annapolis Valley is the most northerly location in maritime Canada where *C. p. picta* occurs in any number. On the basis of the occurrence of these two turtle species, I have included the Annapolis Valley as a northern extension of Herpetofaunal Section 2A. In the Windsor area of the Avon Valley (at the eastern end of the Annapolis Valley), *C. p. picta* is common in ponds formed by the limestone and gypsum sinkholes.

Supporting evidence for the close relationship of the Annapolis Valley to the south-central section of the province comes from the previously mentioned mouse, *Peromyscus leucopus,* which extends up into the Annapolis Valley and Avon Valley from the southwest, having been found as far as the Windsor district but nowhere else in the province (Smith, 1939).

Because of the overall scarcity of turtles and snakes throughout the remainder of Nova Scotia, I have classified it as Herpetofaunal Section 3A. However, there are two pockets in this section that deserve special mention; they appear as black triangles on Map 5.

West of the Annapolis Valley and Avon Valley area and at the same latitude there are no turtles until one gets past the peninsular constriction and into the broader western part of the province. Here, in the limestone and sandstone valleys of the Gay River and Musquodoboit River (the more southerly black triangle) away from the cool sea air, the lakeless terrain has been much given over to cultivation. The herpetofauna is poorer than that of the Annapolis Valley. There are no records of *C. s. serpentina,* but *C. p. picta* is common along several of the meandering streams and rivers. I have no knowledge of the snakes in this area, but to the immediate west in the upper West St. Mary's River, *T. s. sirtalis* and *S. occipitomaculata* are common. However, no *C. p. picta* and only one *C. s. serpentina* (White, pers. comm. 1956) have been found in the latter valley, but *Clemmys insculpta* is well known in the region.

Repeated inquiries and collecting north of the latter area have resulted in finding but one additional climatic pocket. It is located in the environs of the town of Oxford, Cumberland County, which is a rolling sandstone area located just north of the 900- to 1,200-foot-high east-west oriented Cobequid Mountains. In relation to the nearest sea-coasts it is centrally located, and the extensive Jack Pine (*Pinus banksiana*) and Wire Birch (*Betula populifolia*) forest cover of the region testifies to the dry climate. Meteorological data are not available as supporting evidence for the mild climate of this pocket. However, a few apple orchards here occasionally are in bloom at the same time as those in the Annapolis Valley. The Black River and River Philip drain the area, which has five small shallow lakes located on a low divide between these two rivers. This is the only place in northern Nova Scotia where *C. p. picta* has been found. It is rare and confined to these small lakes. On June 21, 1955, I had a guide take me into Slade Lake (locally called Dry Lake because it nearly dries up during some summers). There I saw one adult *C. p.* picta and found six nests which contained freshly laid eggs. I was told of only one larie turtle (undoubtedly *C. s. serpentina*) that has ever been seen locally. However, *Clemmys insculpta* is common in the Black River valley, and *Rana catesbeiana* is common all through the region. *T. s. sirtalis* is common, but evidence is wanting for other snake species.

(e) *Cape Breton Island*

The physiography of Cape Breton Island is a complex of rolling hills and highlands in the southern and eastern parts surrounding Bras d'Or Lake, the large central arm of the sea, while steep-sided gorges are a predominant feature in the plateau region of the north. This latter precipitous 1,500-foot-high formation supports a flora indicative of an intermediate boreal-alpine environment (*See* Smith and Schofield, 1952, for "arctic-montane" plant species from the plateau). The rest of the island has both coniferous forests (particularly along the coasts and on north-facing slopes) and deciduous-coniferous forests (especially well developed in the deep valleys). The southern parts of the island experience temperatures similar to that of the northern mainland; the eastern projection of Cape Breton Island receives a cooling influence from the open ocean; and the northern plateau has the most severe climate of the province.

One striking feature of the Cape Breton Island herpetofauna is the absence of a few species that are common on the mainland, namely turtles of all species, *Rana catesbeiana, Diadophis punctatus edwardsi,* and *Ambystoma jeffersonianum,* though the absence of the latter may be a false impression because of the lack of collecting in early spring. The herpetofauna is otherwise identical to that of Herpetofaunal Section 3A of the adjacent mainland and is therefore designated as derived from Herpetofaunal Section 3A or D3A.

I have been able to find only one report of a turtle for the entire island, and it is a most peculiar one. Dr. A. W. Cameron (mammalogist at the National Museum of Canada) found a large live *Chelydra s. serpentina* on the sea beach at Port Hood in early August of 1953. He carried it to a nearby freshwater pond and released it. It is difficult to know where the animal came from, but people travelling on the mainland do occasionally capture turtles that are seen on the highways and put them in their car trunks to take home. These generally either escape or people release them after a short period in captivity.

The snakes *Storeria occipitomaculata* and *Opheodrys v. vernalis* seem to be generally rare and generally distributed over the island; the latter species had even been seen on the plateau (pers. comm. with E. C. Smith and survey party, 1950). *Thamnophis s. sirtalis* varies locally in abundance from rare to common, with two verbal reports given me in 1950 of great abundance in the southeast region near Loch Lomond. However, these reports were both connected with summer cottages and may merely represent an aggregation of individuals about their hibernaculum, which is under the cottages. I have similar reports from Caledonia in Nova Scotia and Kingsmere in Quebec, where a particular cabin in each locality was infested with Garter Snakes.

A particularly interesting feature of Cape Breton's herpetofauna is the abundance of the newt, *Diemictylus v. viridescens,* of large size in the lakes and ponds on top of the plateau. As very few of these lakes have any fish species, the newts are the dominant aquatic vertebrate in these waters—a unique situation indeed.

(f) *Prince Edward Island*

Slightly to the west of Cape Breton Island lies Prince Edward Island, a Permian sandstone formation of low-rolling relief, rarely exceeding 500 feet in altitude. Except for a few extensive bogs and patches of mixed woodland, it is mostly under cultivation and hence the names "Million Acre Farm" and "Garden of the Gulf." It is evident from early reports, such as Macoun's in 1894, that there was originally a fine forest development of both coniferous and deciduous trees. The island is surrounded by a horseshoe of land, formed by New Brunswick and Nova Scotia, which shelters it from the direct ocean influence. The prevailing summer winds (Putman, 1940) from the west, southwest, and south bring warmed air from the land masses of New Brunswick and Nova Scotia, and make the island warmer in summer than the more southerly but coastal regions of Nova Scotia (*See* Map 3 for mean July temperatures in the Maritimes). There are no large lakes and few small ones, but the province is drained by numerous streams, of which hundreds have been dammed. The ponds and small lakes formed by these dams have been an integral part of the province's topography for generations. Many of the original log dams are rotting away now, and a program is in operation to replace these with more lasting concrete dams because of the rich wildfowl hunting and trout fishing, which have become established in these waters. As would be expected from its small size and low relief, local variations in climate are slight, and meteorologically only a slightly delayed spring can be detected along the north coast and northwest corner of the province.

The situation found in Prince Edward Island is remarkably similar to that of Cape Breton Island, because turtles, *Rana catesbeiana* and *Diadophis punctatus edwardsi,* are absent. Thus both islands are designated as Herpetofaunal Section D3A. Insufficient collecting in this province makes it impossible to say definitely whether *Hemidactylium scutatum* occurs on this island. One specimen has been collected on Cape Breton Island. Snakes seem to be generally rare, except perhaps for local populations of *Thamnophis s. sirtalis.* One distinctive herpetofaunal feature of this island is the overall abundance of *Diemictylus v. viridescens* in the numerous artificial ponds referred to above and in the ponds of the old gravel pits excavated for fill during road construction. I have found this species to be abundant only locally over the rest of Eastern Canada.

(g) *New Brunswick*

The dominant physiographic feature of New Brunswick is the broad shallow St. John River which runs the length of the province from the northwest to the southeast. In this valley and those of some of its southern tributaries is found a broadleaf forest cover while the mountainous and coastal regions of the province support a primarily coniferous forest indicative of a cooler climate. In referring to the softwood nature of the forest cover of the Gulf of St. Lawrence coast of New Brunswick, Halliday (1937, p. 37) says "Climatically, the influence of sea fogs would appear to be marked." The northern half of the St. John River is separated from the marine influence of the Gulf of St. Lawrence by a broad range of mountains of upwards to 2,000 feet in altitude, and it has severe winters and short summers (174 days above 42°F. at Edmundston as compared to

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196 days in the Annapolis Valley (Putnam, 1940). The southern reaches of the river valley are sheltered from the cold Bay of Fundy fogs and air masses by 600- to 1,400-foot highlands along the south coast of New Brunswick. Just north of these highlands in the centre of the southern half of the province and adjacent to the St. John River lies Grand Lake, a 27-mile-long and 18-mile-wide body of water lying in low relief terrain of sandstone, shale, and conglomerate rocks, bordered by numerous marshes, ponds, and weed-choked creeks. The geographic location and the thermostatic regulatory effect of the lake and adjacent river make this region a major warm pocket. It is the only one that has been detected in this province. Halliday (1937, p. 38) mentions that good development of White Elm (*Ulmus americana*) is found especially in the middle of the St. John River Valley, and that the presence of Basswood (*Tilia americana*) and Butternut (*Juglans cinerea*) in the St. John River Valley and around Grand Lake (and, incidentally, not found over the rest of maritime Canada) indicates "more favourable climatic conditions than obtain in other parts of the (Acadian) Forest Region."

The Grand Lake – St. John River area is the only section of this province where *Chrysemys p. picta* and *Chelydra s. serpentina* are known. *C. s. serpentina* is rare, and the scattered populations of *C. p. picta* that I have located are very local in distribution. *C. p. picta* was found at only four of the numerous bays and ponds along the entire shore of Grand Lake. Inquiries made of the local inhabitants and of staff members of the Northeastern Wildlife Station, Fredericton, who have been canoeing through this area for years, verified the herpetofaunal picture. For example, the wildlife officers have been trying to determine if *C. s. serpentina* occurred in the Grand Lake region but had no evidence until one was caught (but not by them) in 1953. The Wood Turtle, *Clemmys insculpta,* is nowhere common but has been recorded from many parts of the province including the Restigouche and Green River valleys in the north (pers. comm. with H. White and Dr. R. F. Morris). Several species of snakes (Table 2) are common in the southern regions of the province and around Grand Lake, but they become scarce in northern parts.

There are three species of amphibians in this province that do not occur in Nova Scotia or Prince Edward Island. One is the stream salamander *Desmognathus f. fuscus,* which is rare to locally common in the lower St. John River Valley as far north as the vicinity of Fredericton. Its range is usually depicted as continuous from the St. John River Valley to the Maine border, but no collecting has yet been done in southwest New Brunswick to substantiate this assumption. A second species is the ubiquitous eastern North American stream salamander *Eurycea b. bislineata,* which occurs commonly in the lower St. John Valley and the Fredericton area but varies from rare to absent in the northern parts of the province. This seems peculiar since farther north it is found in the Gaspé Peninsula at altitudes of up to 2,300 feet. These two salamanders are abundant in the streams on the west side of the Appalachian Mountains in southern Quebec. The third amphibian is the tree frog *Hyla v. versicolor,* which, having been located at but two sites only 5 miles apart, is a rarity in New Brunswick. Both sites are across the St. John River from Fredericton. I have searched for this species during two of its breeding seasons

(1953 and 1955) and have heard it at only one spot but failed to relocate the population in the nearby Nashwaak Valley, from which two specimens were taken for the Royal Ontario Museum of Zoology in 1934. This frog in New Brunswick is separated by 150 miles from the main range of the species, which ends in southern Maine.

Because of the isolated presence in the lower St. John River Valley and the Grand Lake area of *Chelydra s. serpentina, Chrysemys p. picta, Hyla v. versicolor,* and *Desmognathus f. fuscus,* I have designated this Herpetofaunal Section as 2A. Reptiles and *Rana catesbeiana* are difficult to find outside of this Section, and thus much of the rest of the province is classified as 3A, and the line drawn on Map 5 (which includes the Bay of Chaleur lowlands of Gaspé) marks the northern limit of *Clemmys insculpta, D. p. edwardsi, O. v. vernalis, S. occipitomaculata,* and *Rana catesbeiana* for maritime Canada.

(h) ***Gaspé Peninsula***

The mountainous Gaspé Peninsula of Quebec province has a paucity of lakes but possesses numerous streams which deeply dissect the mountains, especially the 3,700-foot-high Shickshock Mountains along the north side of the peninsula. Toward the southwest, this Appalachian formation drops off to 1,000 and 2,000 feet in altitude at the Matapedia Valley and runs southwesterly along the United States – Canadian border and through the southeast corner of Quebec province. The forest of the valleys and lowlands around the Gaspé Peninsula (e.g. the Temiscouata Valley, the Matapedia Valley, and the Bay of Chaleur area) is composed of an admixture of Great Lakes – St. Lawrence Forest and Boreal Forest species with the absence of Hemlock and with a dominance of cedar. With altitude, this changes to a Boreal Forest formation, then through a Black Spruce and White Spruce forest until finally an alpine-tundra condition prevails (Scoggan, 1950).

I have designated this Herpetofaunal Section as 4A because, as in Herpetofaunal Section 4, there are no turtles, bullfrogs, or snakes other than *Thamnophis s. sirtalis.* The only records for the other species of snakes are one for *D. p. edwardsi* at the Gaspé – New Brunswick border and Cox's 1899 report of *O. v. vernalis* from "Gaspé," probably the Bay of Chaleur area, which I have included in my Herpetofaunal Section 3A. The ubiquitous *T. s. sirtalis* occurs all around the peninsula but has never been found higher than 500 to 700 feet (Trapido and Clausen at Ste. Anne des Monts, 1938). It is rather rare, as is evident by Ball's experience (1937). In 1937 Ball spent from June 14 to August 30 conducting a zoological survey of the eastern tip of the peninsula, and during the entire period he saw only eight *T. s. sirtalis.* Likewise *Diemictylus v. viridescens* is known from the periphery of the peninsula and is common in some areas but has not been seen above 1,000 to 1,200 feet of altitude. *Bufo americanus, Rana septentrionalis,* and *Eurycea b. bislineata* are common and have been observed by this writer at 2,000 feet (Lac Vison) and the last species also at 2,300 feet (Trapido and Clausen at Lac aux Américains). At Lac au Claude, about 2,200 to 2,400 feet in altitude, the warden told me that "frogs" were heard in spring at the south end of the lake, and at the time I heard one *Bufo americanus* calling. There is a dense Black Spruce forest at this altitude. *Ambystoma maculatum* has been taken at

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700 feet, *Ambystoma jeffersonianum* at 1,000 to 1,200 feet, *Rana sylvatica* at 3,700 feet, and *Hyla c. crucifer* at 1,000 to 1,200 feet of altitude. Earlier spring collecting should be done in these mountains, for then a very interesting comparison could be made of the distribution patterns with altitude in the Gaspé, with the distribution patterns with latitude of the same species in Quebec and Labrador (Taxonomic comparisons on the subspecific level would also be of significant interest.).

(i) *Anticosti Island and Newfoundland*

Before discussing northern Quebec and Labrador, the herpetofauna of Anticosti and Newfoundland should be mentioned since they were derived from Herpetofaunal Sections 3 and 3A respectively. Neither island had a native herpetofauna, and what species exist there now were introduced by man within the past hundred years.

Climatically the complex physiography of Newfoundland helps create three areas which are warmer than adjacent regions. These pockets are the Humber River Valley at Dear Lake, St. Georges on the west coast, and the centre of the Avalon Peninsula in the southeast part of the province (Hare 1952). There is an abundance of suitable aquatic habitats available. However, as far as is known only *Rana clamitans* has been accidentally introduced from Nova Scotia to St. John's about 1850, according to Johansen (1926). This species has since spread over the Avalon Peninsula, and when I was there in 1949 this frog was common in the numerous ponds and streams in the southern part of that peninsula. Logier and Toner (1955) report a specimen from Glovertown, 75 miles north of the Avalon Peninsula, but there seems to be no information as to whether this population was introduced from the Avanlon Peninsula, or if it has simply migrated that far.

Anticosti Island is a large Ordovician and Silurian limestone formation of low relief situated at the mouth of the St. Lawrence River. There are many shallow streams and ponds which dry up considerably in summer leaving wide marl beaches (Johansen, 1924). The climate is rather uniform, and it is unlikely that any pockets will be found. In 1899 frogs from Quebec City were deliberately introduced in an effort to combat the plagues of biting flies on the island. This original population has spread eastward from the site of introduction which was ponds in the vicinity of Port Menier (Ellis Bay area and neighbouring Lake St. George, says Johansen, 1926), but exactly how far east has not been determined. As far as I know, no herpetologist has collected on Anticosti Island, and all we know of its introduced frog population is that it is composed of at least two species, namely *Rana p. pipiens* and *Rana septentrionalis*.

(j) *Quebec and Labrador*

North of Lake St. John lies the vast territory of Quebec-Labrador or Ungava-Labrador. Geologically it belongs to the great Precambrian Shield formation and is a region of innumerable lakes, rivers, and bogs. It rises rather abruptly along its southern border (particularly along the north shore of the Gulf of St. Lawrence where it forms the Laurentian Scarp) to altitudes of 1,000 to 3,000 feet and then gently slopes toward the northwest and into Hudson Bay and Ungava Bay. Between Lake St. John and the tree-limit line near Latitude 57°N. to 59°N. are 700 miles of Boreal

Forest. However, important climatic discontinuities exist in this overall gradual south to north gradation. These milder sections are the north shore of the Gulf of St. Lawrence; the Hamilton River Valley – Lake Melville area; and the upper reaches of the Kaniapiskau River in Ungava (the Fort MacKenzie area).

Along the north shore of the Gulf of St. Lawrence from Sept Iles to Natashquan at the foot of the 2,000-foot-high Laurentian Scarp is a wide marine terrace several miles in width. The rivers flowing from the scarp have cut deep valleys through these sedimentary deposits, and in these protected valleys several species of amphibians and reptiles reach their northern limit. These species are *Thamnophis s. sirtalis, Plethodon c. cinereus, Eurycea b. bislineata,* and *Rana clamitans.* Collections from Lake Mistassini and the James Bay area indicate that the limit line for these species west of the Laurentian Scarp is roughly the latitude of southern James Bay. I have called this Herpetofaunal Section 5. This Section may also mark the northern limit of the continuous range of *Ambystoma jeffersonianum, Rana p. pipiens,* and *Hyla c. crucifer,* for although reported from farther north they have not been collected in the intervening territory at sites where other species have been taken.

Three hundred miles north of this low coastal plain is a warm pocket in the valley of Lake Melville and its tributary rivers. The trees of the forest are of commercial size (Hare, 1950, claims this to be the greatest untouched source of pulpwood), while the surrounding country has an arctic type of vegetation with an almost complete absence of White Spruce and Balsam Poplar which are so prevalent in the valleys. Halliday (1937, p. 16) says that here protection is certainly one of the controlling factors in determining tree cover and growth quality. The frog *Rana p. pipiens* and the salamander *Ambystoma jeffersonianum* reach their northern limit at Lake Melville. There are no representative specimens of *Plethodon c. cinereus* or *Hyla c. crucifer* from this section. However, I have received verbal reports of these species. Therefore it is possible that they, together with the previously mentioned two species, have relict populations in the Lake Melville area. I therefore designate this region, tentatively, as Herpetofaunal Section 5A.

North of Section 5A only three species have ever been collected. One, *Bufo americanus,* is common as far north as Menihek Lake, Latitude 54° 30' N., but is very rare at Knob Lake some 40 miles farther north. The limit of this toad marks Herpetofaunal Section 6.

The remaining two species are *Rana septentrionalis* and *Rana sylvatica.* The former has been taken rarely at Latitude 57° N., which is about 50 miles south of the tree-line, and the latter species is relatively common north to the tree-line from Labrador to Alaska. These two frogs are the only representatives for Herpetofaunal Section 7.

A summary of each Herpetofaunal section is presented in Table 3, and an overall picture of the herpetofauna of Eastern Canada can be gained from this table. The richest fauna is in the south and west of the Appalachian range, while that of Nova Scotia and New Brunswick is second with approximately two-thirds as many species. The derived faunas of the four Gulf of St. Lawrence Islands differ sharply in that two islands have exceptionally few species and two have nearly as many species as the mainland. In the higher altitudes and latitudes of the region there is a sharp reduction in the numbers of species, especially of reptiles.

Further studies in the Gaspé peninsula would make it possible to accurately delineate, altitudinally, Herpetofaunal Sections 5A, 6A, and 7A, because the same species occur there as in northern Quebec and Labrador.

Factors Limiting Distribution

The factors involved in limiting the ranges of amphibians and reptiles have not been well studied. Oliver (1955, p. 135) says "To be sure, we know the effect of extreme conditions and some of the gross results of certain variations in these factors, but we do not know the exact requirements of a single species for any one factor throughout the life of that species." I feel, however, that discussion of them is warranted here, for a knowledge of these factors is rather essential to the interpretation of the past and present distribution patterns of the eastern Canadian amphibians and reptiles. This digression serves as an analysis of the foregoing section on zoogeography and at the same time as a preamble to the following section on postglacial migrations of amphibians and reptiles.

Through the years, various limiting factors have been deduced and then often assumed to be correct, without undergoing experimental verification. For instance, in discussing the limiting factors affecting the skink, *Eumeces fasciatus*, Schmidt (1950) says "The range of the common five-lined skink, *Eumeces fasciatus*, of the southeastern United States is strictly limited to the east and south by the Atlantic Ocean and the Gulf of Mexico. The northern border of the range is no doubt limited on one hand by the length of the favourable summer season and on the other by the degree of winter cold .... To the west, the limiting factors must be principally the presence of suitable cover, *Eumeces fasciatus* being found mainly under loose bark and under or in rotting logs, and in competition with other species. The primary physical factors are reduced rainfall and increased aridity, which cause the forest to give way to grassland. Competition with climatically adjusted and rock-crevice inhabiting species of the same genus appear to be an effective biotic limiting factor." However, in spite of these reasonable deductions it is still uncertain in the north of this species range which of the two factors (1) severity and depth of freezing of the soil in winter (affecting hibernating individuals) or (2) insufficient warming of the soil in summer (affecting development of eggs) is the more important factor. Again, in the west of its range, it is not known what the true relationship is between the plausible limiting factors of (1) lack of forest, (2) competition with prairie lizards, and (3) reduced moisture.

Moore (1939, 1940, 1942, 1949, and 1952) has made a major contribution in this respect through his determinations in the laboratory of the developmental rates and the limits of temperature tolerance of developing eggs of six species of frogs from eastern North America, namely *Rana catesbeiana*, *R. clamitans*, *R. palustris*, *R. p. pipiens*, *R. sylvatica*, and *R. septentrionalis*. Moore (1939) found that the more northern species developed faster at cold temperatures. With the exceptions of *R. p. pipiens* and *R. septentrionalis,* he found that specimens of the same species from different latitudes had the same range of temperature tolerance (1942). A comparison of these figures with the geographic range showed that each species was limited in the north and south of its range by environmental temperatures, which exceeded the range of temperature tolerance of the developing eggs. Thus in the north the daytime temperatures may be such that adult frogs could feed and breed, and escape the cold nights by retiring to the pond bottoms each evening, but their eggs would be exposed to the evening drop in temperature and thereby would be destroyed. Piersoll, 1929, has shown that a drop in temperature to 39.2°F. (4°C.) will cause stratification in the newly laid eggs of *Ambystoma jeffersonianum* and at a temperature of 37.4°F. (3°C.) no development takes place in eggs of either *A. jeffersonianum* or *A. maculatum.* However, the adults are tolerant of greater cold than this and have been found active in ice-covered ponds. In these cases, then, it is the minimum nocturnal temperature (during the egg-laying season), through its effect on the normal development of the eggs of these amphibians, that limits their northward spread. To what extent this is true of other amphibians and reptiles is as yet unknown, but the unprotected eggs of the egg-laying species seem to be the vulnerable stage in their life-history.

The two exceptions to these general findings of Moore are *R. p. pipiens* and *R. septentrionalis.* The former species (Moore, 1947) has a variety of embryonic temperature tolerance limits and metabolic rates according to the regional climatic conditions. Thus *R. p. pipiens* from Vermont develops faster at cool temperatures than do specimens from Mexico; in fact, crosses between individuals of this species from these two latitudes result in non-viable abnormal embryos (1947). Thorson (1950) comments on a similar relationship in marine invertebrates where eggs and larvæ of northern cold-adapted species develop in the same time as southern species of the same genera. The cold temperatures do retard development in the north but not so much as would be predicted from the Q_{10} Rule, because there apparently is a compensating increase in the metabolic rate of these northern organisms. Dehnel (1955) and Bullock (1955) have experimented with many invertebrates and determined the physiological temperature ranges and metabolic rates for northern and southern populations of the same and related species. These workers have observed many cases of apparent temperature-independent growth rates in both southern and northern populations and point out that the Q_{10} Rule is inapplicable in such instances. As Bullock states, "The wide distribution and demonstrated natural occurrence of acclimation and related rate compensations for temperature bespeak a large-scale role in ecology and evolution."

In 1950 Moore reported on his geographical study of the second species, *R. septentrionalis.* However, he has reported wrongly on several points. He gives the range of this species as 43°N. to 50°N., but 57°N. is correct (Distribution Map 23). His experimental material came only from New York State, and the temperature tolerance limits determined were 14°C. to 31°C., just one degree below that of *Rana catesbeiana* (15°C. to 32°C.). This latter species extends the least far north of any northeastern ranid. Now, since *R. septentrionalis* ranges nearly as far north as *R. s. sylvatica,* which has a temperature tolerance range of 2.5°C. to 24°C., then *R. septentrionalis* eggs must also have a similar temperature tolerance range in northern Quebec. This means that populations of *R. septentrionalis* in New York State and Ungava have different temperature tolerance limits, a situation which is identical to that found in *R. pipiens*.

There is additional evidence for this wide difference in embryonic temperature tolerance in populations of *R. septentrionalis*. It is well known that the species of ranids which emerge earliest in spring and lay their eggs at that time, such as *R. s. sylvatica*, are tolerant of low temperatures and therefore can develop in the cold waters of high latitudes and altitudes. It is significant therefore that *R. septentrionalis* in New York has its peak of laying during July (June 24 to July 30, according to Wright and Wright, 1949, and Moore, 1952), yet my own work in Quebec and Labrador showed that this species breeds and lays in early spring at the same time as *R. s. sylvatica*, *Hyla c. crucifer*, and *Bufo americanus* (In New York State, breeding dates for *R. sylvatica* according to Wright and Wright are March 19 to April 30). First dates in 1952 for *R. septentrionalis* at Sept Iles, Quebec, were the first week of June; at Mile 134 (on the Quebec-Labrador Railway), the week of June 17 to 23. In these latitudes, therefore, it must have developmental temperature tolerance limits that approach those of *R. sylvatica*, and not *R. catesbeiana* as Moore has determined for New York populations. Baker in his "Evolution of Breeding Seasons," 1938, cites several species of birds in Ceylon as examples of animals which breed at different times of the year within their range. The fact that the monsoon period occurs at different times of the year on the two sides of this island may account for the variation. *R. septentrionalis* is unusual in that it breeds during July in the southern part of its range (Latitude 45°N.) and breeds during June farther north (Latitude 52°N.). Generally a species breeds at successively later dates toward the north.

R. septentrionalis must be a very labile species as regards temperature tolerance. This is true also of its metabolic rate, as is indicated by Moore's experiments on the number of hours it took the embryos of the species *R. clamitans*, *R. catesbeiana*, and *R. septentrionalis* at 19.8°C. to pass from stage 3 to stage 20 (stages from Pollister and Moore, 1937). It took *R. clamitans* 112 hours, *R. catesbeiana* 131 hours, and *R. septentrionalis* gave readings of 119, 120, and 137.5 hours. Moore says (p. 16): "I am at a loss to explain this great variability in *R. septentrionalis*. I have not observed differences of this magnitude in individuals of other species when adults are from the same locality." The evidence is, then, that there is great individual variation of embryonic temperature tolerance and rate of development in single populations of *R. septentrionalis* and that through natural selection the populations in Quebec and Labrador consist of individuals whose eggs are tolerant of low temperatures.

The question now arises that if this is such a labile species, why does it not range over most of North America as does *R. p. pipiens*? Moore suggests that it is in competition with *R. catesbeiana* and cannot penetrate southward into the latter's range. To support this contention, he says (p. 10) that the ranges of the two species overlap only in southeastern Ontario and that they usually are not found in the same locality. My own field work disproves both these statements. First, the species overlap extensively in Ontario, southern Quebec, New Brunswick, and Nova Scotia; and secondly, I have collected both species side by side on many occasions in Ontario, New Brunswick, and Nova Scotia. There is, therefore, no concrete evidence of what factor limits *R. septentrionalis* at the south and west of its present range.

It is evident that the study of limiting factors affecting the distribution of amphibians and reptiles is yet in an embryonic stage. Nevertheless, I would like to point out in this section the evidence for certain important limiting factors.

The amphibians and reptiles of Eastern Canada reach their northern limits in this region, and the dominant limiting factor is temperature. This is because amphibians and reptiles are poikilothermous animals and cannot long remain active at low temperatures such as prevail in northern Canada. This necessitates a hibernation period of about five months in southern Canada and eight months in northern Quebec. A gross correlation between the major orders of the amphibians and reptiles and their distribution in Eastern Canada is evident when their ranges are plotted, as on Map 6. Lizards form the most southerly group; only one species is found in Eastern Canada. Fitch (1954, p. 21) says "As compared with its reptilian associates in northeastern Kansas, *Eumeces fasciatus* is outstanding in its ability to become active and carry on normal activities at relatively low air temperature." Its preferred body temperature is approximately 30° C. (86°F.) according to Bogert (1949, p. 205). Fitch's figures (p. 57) indicate that a drop in temperature to 10°C. (50°F.) would be lethal. In Canada such environmental temperatures as required by this species are realized only in southern Ontario. Reference to Distribution Map 38 illustrates how this species skirts south of the eastern Ontario highlands of the Algonquin Park region, and again skirts west of the Adirondacks, Allegheny's, and south of the Catskill and Blue mountains of New York and Pennsylvania, and south of Green and White mountains, and then extends northeast along the low coastal plain of the New England States. Turtles range slightly farther north but are limited by the foothills of the Canadian Shield in southern Quebec. They skirt south of the White Mountains on the Maine-Quebec border and extend along the southeast side of the Appalachian mountains to the latitude of northern New Brunswick. They do not occur in the mountainous Gaspé Peninsula. The limit line for all snake species, except *Thamnophis s. sirtalis,* lies very close to that of the turtles, about 50 miles farther north. There is a northward jump from here, averaging 200 miles, to the limit of the salamanders. Peculiarly enough, the Garter Snake, *T. s. sirtalis,* has a similar latitudinal limit. The usual explanation for this is (1) being the first reptile to emerge in spring it must be cold tolerant and therefore would be expected to extend farther north than any other reptile (This is similar to the relationship that *Eumeces fasciatus* holds to other lizards). (2) It is ovoviviparous, and therefore the female can seek out the warmest microhabitats during the sunny hours and thereby obtain a maximum number of hours of incubation for her embryos. The eggs of oviparous snakes, on the other hand, must remain buried in one place and are subject to night chillings or even to freezing at high altitudes and latitudes. The northern limit of frogs is nearly 400 miles north of the salamander line. This is rather perplexing, because adult salamanders and especially their larvæ are often active all winter even beneath iced-over streams and ponds, while tadpoles and frogs invariably become inactive during cold weather. Perhaps the soil

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temperature and permafrost inactivate the adult salamanders which spend much of their life-history in the soil, whereas the frogs live in the water and along the margins of ponds. Temperature tolerance limits of the salamander eggs may well be a prime limiting factor.

The occurrence of isolated species populations in protected valleys (viz. Lake Melville area, Labrador; St. John River – Grand Lake area, N.B.; Gatineau Valley, Que; Oxford, N.S. etc.), in the warm southern latitudes of Nova Scotia, and away from the cool sea-coasts of the Maritimes is further indication of the temperature sensitivity of amphibians and reptiles.

Since temperature is probably the dominant limiting factor, it seems reasonable that some kind of environmental temperature index could be calculated from long term meteorological data. With such an index, one could determine the index for an area from which weather data were available and from a comparison with a known area of similar index could predict what amphibians and reptiles should be found there. It could also be consulted where introductions of amphibians and reptiles were being contemplated. An Environmental Temperature Index for the amphibians and reptiles of Eastern Canada was derived through multiplying the Length of Growing Season by the Mean July Temprature. The reasons for using these figures are sveral. One is based on the fact that amphibians and reptiles come out of hibernation when the mean daily temperature reaches 40°F. to 50°F., depending on the species concerned (Morgan, 1939; Wright and Wright, 1949; Bishop, 1941; Fitch, 1954). The Length of Growing Season, which is readily available from meteorological offices and several publications (Putnam, 1940, and Putnam and Chapman, 1938), is the number of days that the mean daily temperature is above 42°F. This is believed to represent the duration of the period of plant growth. At the same time it approximates the length of the summer activity period of amphibians and reptiles. This figure then gives us the length of summer season in which amphibians and reptiles can remain active. The activity and growth of amphibians and reptiles is proportional with limits to the environmental temperature. That is, eggs, young, and adults develop and grow faster at warm temperatures. Cowles and Bogert, 1944, observed that the Eastern Garter Snake (*Thamnophis s. sirtalis*) and the Great Plains Garter Snake (*Thamnophis radix*) kept at a constant temperature of 80°F., fed, defecated, and shed skin more frequently than did individuals of the same species kept at 70°F. In southern Michigan, Blanchard and Blanchard (1940) found that the period of embryonic development for *Thamnophis s. sirtalis* varied from 87 to 116 days. The shortest period occurred during an extremely hot summer, and the longest during an unusually cool one. The difference in embryonic-development time amounted to four days per degree of temperature. Reaumur (1735) laid the foundation for such modern work on the summation of temperatures when he discovered that the sum of the mean daily temperature made a constant for any given phenological period. Therefore in theory, a poikilothermous species should thrive equally well in an area which had a short but warm summer season or in an area with a longer but slightly cooler season. With few exceptions in Eastern Canada, July is the hottest month. I have therefore chosen the mean temperature of this month as representing a figure for the relative amount of heat available during the summer for the development of amphibians and reptiles in an area. By multiplying the Length of Growing Season by the Mean July Temperature for two slightly dissimilar areas, such as just outlined above, a similar product should result, and similar herpetofaunas should be expected to occur in the two areas. This was actually tested by comparing the environment at the northern limit of the species *Thamnophis s. sauritus* and *Emys blandingi,* which have range limits in eastern Ontario and south-central Nova Scotia (*See* Distribution Maps 42 and 31). The Length of the Growing Season for Ottawa and Almonte in eastern Ontario is 190 days and 192 days respectively. For Springfield in south-central Nova Scotia it is 199 days, but the two species nevertheless are rare in Nova Scotia. Examination of the mean July temperature for these areas shows that Springfield with 66°F. is cooler than eastern Ontario with 69.6°F. and 68°F. When the Environmental Temperature Indices were calculated, they showed a remarkable similarity; Ottawa, 13,224; Almonte, 13,056; and Springfield, 13,134. The Environmental Temperature Indices for Eastern Canada are plotted on Map 7 in company with the Herpetofaunal Sections limit lines and for convenience have been reduced to 13.1, 12.6, 11.0, etc. Note how the Environmental Temperature Indices conform rather well to the Herpetofaunal Sections:

Herpetofaunal Sections	Environmental Temperature Indices
1	15 to 13
2, 2A	13 to 12
3, 3A	12 to 11
4, 4A	11 to 10
5, 5A	10 to 8
6	8 to 6
7	6 to 5

This rather simply derived but seemingly effective herpetofaunal Environmental Temperature Index could be refined, but this is not warranted since the significance of any figures after the decimal is rendered questionable by certain meteorological discrepancies. There is a possible margin of error of several degrees Fahrenheit between the temperatures of the microclimatic environment of the meteorological recording instruments and the microclimatic environment of the local amphibians and reptiles. In the first place, the meteorological instruments which record the data are about four feet off the ground, whereas the amphibians and reptiles mostly dwell at ground level, and therefore temperature readings for an area cannot be directly related to the environment of the local herpetofauna. Secondly, the meteorological instruments may be located in a valley, on a hilltop, on a rooftop, over sand, over rock, on a north or any other directed slope exposed to winds or protected by buildings. Longley (1954, p. 33) points out that the temperature readings at McGill University and Dorval Airport, both only a few miles apart on Montreal Island, differ during spring and autumn by an average of 3°F.

The Environmental Temperature Indices for the coastal regions are somewhat misleading because, although the temperature is above 42°F. for as long as 204 days (Yarmouth, N.S.), it is not much higher and is still too cool for normal development of turtles and some species of snakes. Another factor is that, although the maximum temperature for the day may be recorded as 70°F., the morning and evening fogs can restrict the 65°F.

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to 70°F. temperatures to a period of only a few hours. Farther inland, however, the day maximum may also be 70 degrees, but the clear skies here result in a much longer period of 65°F. to 70°F. temperatures than on the coast, which of course is of vital importance to poikilothermous amphibians and reptiles.

Disregarding these coastal figures, the Eastern Painted Turtle, *Chrysemys p. picta,* is found in areas with an Environmental Temperature Index of 12.0 or more. At an index number of 13.0 it is common to abundant, as in eastern Ontario and southern Nova Scotia. It is of interest to note that the Environmental Temperature Index in Nova Scotia at Mount Uniacke, in the peninsular construction at Windsor-Halifax, is only 11.1, and *C. p. picta* does not occur there. To the northeast of Mount Uniacke the Environmental Temperature Index rises to 12.1 at Upper Stewiacke, and just south of this region populations of *C. p. picta* do occur.

There are very few records of turtles from the high country of Ontario in the Algonquin Park region. This is evident in Herpetofaunal Section 2 where the section makes a wide circuit around the area. Mr. E. B. S. Logier, of the Royal Ontario Museum, says (in litt.) that expeditions from that museum have spent weeks at a time in the park, and all have reported turtles as rare, and "*Chelydra serpentina* appears to be the only one of even moderately common occurrence." He goes on to say that the only other species recorded is a single *Chrysemys picta marginata* taken at the extreme southern border of the park at an altitude of about 1,250 feet. The Environmental Temperature Index determined for this area is 11.1 which also seems to mark the limit for turtles in other regions of Eastern Canada. There are other species whose limit lines follow an Environmental Temperature Index isopleth rather closely, and they are:

Species	Environmental Temperature Index at Northern Limit
Ambystoma jeffersonianum	8.5
Plethodon cinereus	8.5
Bufo americanus	6.0
Rana sylvatica	5.2
Rana catesbeiana	12.0
Chelydra serpentina	11.0
Chrysemys p. picta	12.0
Thamnophis s. sirtalis	8.3
Storeria occipitomaculata	11.3
Opheodrys v. vernalis	11.3
Diadophis punctatus edwardsi	11.5

Although the eleven species listed above fit the isopleths of the Environmental Temperature Index and thereby substantiate its applicability, the remaining species are inconsistent in this respect. There are two probable explanations for this: (1) Insufficient knowledge of the species' distribution owing to lack of collecting and (2) some effective barrier other than temperature. As distribution of several of these species is well known, barriers other than temperature must be involved. These barriers will now be discussed, although it is not understood precisely how some of them function as such.

There are six species against which the waters of the Great Lakes and St. Lawrence River have served as an efficient barrier to their distribution. Two of these species are the stream salamanders, *Desmognathus f. fuscus* and *Gyrinophilus p. porphyriticus*, which occur along the south shore of Lake Erie and Lake Ontario and in many of the streams in New York State and Quebec Province that flow northward into the St. Lawrence. This constitutes a 600-mile front along the south side of Lake Erie and Lake Ontario and the St. Lawrence River with a range in the Environmental Temperature Indices of from about 15.0 at Lake Erie to about 12.0 near Quebec City. However, years of collecting have shown that they have managed to cross this system only at the Niagara River, and occur only along the Canadian side of that river. An isolated 1934 record from Ottawa for *Gyrinophilus p. porphyriticus* indicates that it has crossed at this latitude, but I have searched in vain along streams in the Ottawa Valley for additional specimens and now feel that the original specimen could be the result of an accidental or deliberate introduction.

The exact manner in which this water barrier functions is unknown. It should be pointed out that *Eurycea b. bislineata*, another stream salamander, often found in company with the above two, is equally common both north and south of the Great Lakes – St. Lawrence River system. Perhaps the habitat preference of the first two-mentioned salamanders prevents them from crossing at other points. They both inhabit the margins of small streams and avoid the shores of large rivers and lakes. The prevalence of strong wave- and ice-action and the high temperature during summer in the littoral zone may be limiting factors in this case. In addition, they are lungless salamanders and cannot float, and therefore they would have to swim the entire crossing or walk across on the bottom, where the carbon dioxide concentration might well be lethal. The ubiquitous *Eurycea b. bislineata*, on the other hand, is found in rivers (Ottawa and Rideau of Ontario and the St. John of New Brunswick), and Bishop (1941, p. 292) says that the larvæ were fairly common among the stones along the shore of Lake Eaton, New York, where, he writes, they must have been subjected to considerable wave-action during storms.

The dispersal of two species of snakes, *Coluber constrictor* and *Thamnophis butleri*, has been hampered by these waters. These snakes occur along the United States side of lakes Huron, Erie, and Ontario. However, they have managed to cross only in the Lake St. Clair area and are known only from two localities each within 50 miles of the Michigan border.

The final two species of the six that have found these waters a formidable barrier to their distribution are turtles. One is the terrestrial Box Turtle, *Terrapene c. carolina*, which occurs along the United States shores of Lake St. Clair, Lake Erie, Lake Ontario, and the upper St. Lawrence River Valley to near the Quebec border but has never been recorded from a Canadian locality. The same is true of the bog-dwelling turtle *Clemmys muhlenbergi*, though its range along Canada's border is confined to the east end of Lake Erie and eastward along the south shore of Lake Ontario. Temperature is not a factor here, for this species has been taken in the Appalachians at altitudes of "well over 4,000 feet" (Carr, 1952, p. 131). Perhaps strong habitat preference is the important limiting factor affecting these two species.

There is perhaps no better illustration of the effectiveness of a water barrier than that exemplified by the distribution pattern of the frog *Pseudacris nigrita triseriata* along the Ottawa and St. Lawrence rivers. *P. nigrita triseriata* occurs abundantly on the south side of the Ottawa River from (at least) South March (10 miles west of Ottawa) eastward to the junction with the St. Lawrence River at Montreal Island. Nevertheless, it has crossed only in the area of Hull, Quebec, and here it has penetrated northward up the Gatineau Valley for 20 miles to Wakefield. At the junction of the Ottawa and St. Lawrence rivers the species has gained Ile Perrot over a 1,000-foot width of river (or over two 500-foot jumps via Ile aux Pins), but it has not crossed the second 1,000-foot river barrier which would put it on Montreal Island. Across the St. Lawrence River from the city of Montreal I have heard choruses of this little frog in the swamp at the foot of the Jacques Cartier Bridge at Montreal Sud. The river here is about four-fifths of a mile wide. I could not find *P. nigrita triseriata* along the north shore of either the Ottawa or St. Lawrence rivers in the Montreal region. Why these rivers serve as such a formidable barrier to this frog and not to other frogs, is not yet known.

In the Maritime Provinces there is a definite but as yet undefined faunal and floral barrier in existence between New Brunswick and Nova Scotia. In brief, the situation is that many organisms which live successfully in the climate of New Brunswick do not occur in Nova Scotia where one would expect them to be, even though the latter province is more southern and has a milder climate. The two amphibians *Hyla v. versicolor* and *Desmognathus f. fuscus* are found in the lower St. John River of New Brunswick but are absent from southeastern New Brunswick and from all of Nova Scotia. Evidence will be presented in the discussion of the postglacial period supporting the contention that the climate in Eastern Canada was much warmer 4,000 years ago. The climate, therefore, at the New Brunswick – Nova Scotia border could not have been a barrier at that time even though it may be now. More striking is the distribution of *Eurycea b. bislineata,* which ranges in Eastern Canada from southern New Brunswick to altitudes of 2,300 feet in the Gaspé Peninsula and along the north shore of the St. Lawrence River to Latitude 51°N. but has not crossed the Isthmus of Chignecto into Nova Scotia. However, both *Desmognathus f. fuscus* and *Eurycea b. bislineata* are stream salamanders, and possibly the salt marshes and creeks and the freshwater bogs that constitute this isthmus are unsuitable habitats and therefore function as barriers. Similarly the preference of *Hyla v. versicolor* for deciduous trees may exclude it from the coniferous forest that predominates over southeastern New Brunswick and the Isthmus of Chignecto.

The distribution of the flora and fauna of the Maritimes has received considerable attention, and it is interesting to note how many other organisms besides the above three amphibians have ceded to this southeastern New Brunswick barrier. The crayfish, *Cambarus bartonii,* which occupies the same stream habitat as *D. f. fuscus* and *E. b. bislineata,* has been collected from north and central New Brunswick but never from the southeast corner of the province, and it is absent from Nova Scotia and Prince Edward Island (Ganong, 1898, p. 54, and pers. comm. with Harley White, 1956). Of the 44 species of fresh-water fish known to occur in New Brunswick, only 33 were found in Nova Scotia by Livingston (1950–51) during his 1947–50 survey of the province. The trees—Basswood, Silver Maple, and Butternut—are found in south and central New Brunswick but have not penetrated into Nova Scotia (Roland, 1944–45, p. 17).

What is more surprising is that several species of flying animals, namely butterflies and birds, are similarly affected by this barrier. Ferguson (1952–53, p. 176) points out that the two salt-marsh species of butterflies *Lycaena dorcas dospassosi* and *Coenonympha inornata inpisiquit* occur in northern New Brunswick near Bathurst, but although the same habitat conditions prevail in many parts of Nova Scotia these butterflies are absent. Similarly, he notes that *Incisalia lanoraiensis* dwells in the spruce bogs of Maine, New Brunswick, and Quebec, yet it seems to be absent from bogs in Nova Scotia.

W. E. Godfrey (ornithologist at the National Museum of Canada) has kindly supplied me with the following information on distribution patterns of birds in Maritime Canada. The Red-shouldered Hawk, American Coot, and Crested Flycatcher have all been recorded as breeding in southern New Brunswick, but in Nova Scotia only the latter species has been recorded and but once. Birds which are common summer residents in New Brunswick and are either absent or very rare in Nova Scotia are the Killdeer, Whip-poor-will, American Three-toed Woodpecker, Eastern Phoebe, House Wren, and Western Bluebird. Two of these species deserve special mention. One is the Killdeer which occurs as far north as Bathurst in New Brunswick. It has crossed the marine barrier of the Northumberland Strait (9 miles wide at the narrowest point) to invade Prince Edward Island, yet it is exceptionally rare in Nova Scotia, which is more southerly than those two provinces. The other species of interest is the American Three-toed Woodpecker, common from Labrador to New England including New Brunswick, but absent from Nova Scotia.

From the foregoing information it is apparent that a real and selective barrier exists in the area of the New Brunswick and Nova Scotia border which affects the dispersal of both flora and fauna into Nova Scotia. It would be of value to have more distributional data for small mammals and both terrestrial and fresh-water invertebrates from this area.

One of the most effective and well-recognized barriers to amphibians is salt water. Any prolonged immersion is fatal. In contrast, the relatively impervious skin of reptiles makes it possible for them to tolerate prolonged exposure to salt water. Thus is explained the fact that reptiles and rarely amphibians populate the off-shore islands of the continents. Of the four large islands off Canada's east coast, the two northerly, Anticosti Island and Newfoundland, have no native amphibians or reptiles and only a few introduced species of frogs. The coast adjacent to these two islands is the north shore of the Gulf of St. Lawrence where one snake, three salamander, and five frog species are known to occur. I suggest that the salt water has barred the amphibians from crossing these islands and that the cold temperature of the water along this coast (14°C. in July to

August, and go as low as 4°C. in August as is shown in fig. 6, Lauzier *et al.*, 1951) would probably benumb any snake attempting the swim. Even those turtles, snakes, and crocodilians that are marine live only in warm climates.

In contrast, the other two islands, Prince Edward and Cape Breton, have the same herpetofaunal elements as are common in the adjacent mainland of New Brunswick and Nova Scotia, except for *Rana catesbeiana,* all species of turtles, and possibly the snake *Diadophis punctatus edwardsi.* The latter species has not received sufficient attention as yet to risk a definite statement of its presence or absence .... The 15 amphibian and reptile species common to these islands and the adjacent mainland (which has 20 species) indicate that at one time there was a land connection and that *R. catesbeiana, D. punctatus edwardsi,* and the common eastern Canadian turtles *Clemmys insculpta, Chelydra s. serpentina,* and *Chrysemys p. picta* arrived in the region after the land bridge had disappeared (This theme is developed fully in the discussion of postglacial aspects). I suggest that the salt water has barred the frog *R. catesbeiana* and that the cold temperature of the water (July temperature 19°C., fig. 4, Lauzier *et al.*, 1951) serves as the prohibiting factor to turtles.

The distribution pattern of the mammalian faunas of these four large islands is decidedly similar to that of the herpetofauna. Anticosti Island and Newfoundland have a paucity of terrestrial mammalian species as compared to the adjacent mainland of Quebec and Labrador (A. W. Cameron, Ph.D. thesis, McGill, 1956).

The former island has but five known native mammals (Red Fox, Otter, Deer Mouse, Black Bear, and Pine Marten), and Newfoundland has a mere dozen (Caribou, Black Bear, Red Fox, Otter, Pine Marten, Weasel, Beaver, Muskrat, Lynx, Arctic Hare, Meadow Mouse, and Wolf). Prince Edward Island and Cape Breton Island, on the other hand, possess all the mainland species including the many small rodents and insectivores, except the Raccoon, Striped Skunk, Porcupine, and Woodchuck.

Insufficient sources of food as a factor that limits the northward spread of amphibians and reptiles is unlikely. The plants and insects that the turtles eat occur much farther north. The insects and other invertebrates that salamanders and frogs prey upon are abundant throughout Eastern Canada. Invertebrates, frogs, and small mammals are common north of the range limit of their snake predators.

In summary, from the available evidence of the distribution patterns of amphibians and reptiles in Eastern Canada there exist various barriers to dispersal in different parts of a species range. The factors which most influence or limit distribution are low temperatures, large rivers and lakes, salt water, cold salt water, habitat preference, perhaps interspecific competition, and unknown factors such as those evident near the New Brunswick – Nova Scotia border. However, even in cases where the limiting factor is known or suspected, the precise way in which it functions is poorly understood.

Herpetofauna during the Postglacial Period

During the Pleistocene Epoch all of Eastern Canada was subjected to at least four major glaciations (Flint, 1953, p. 210). The Wisconsin Glacial Stage commencing about 55,000 years ago was the last and the most extensive (Flint, 1953, pp. 242, 532). Minor shrinkages and expansions followed within the third and last expansion (Mankato Substage) occurring about 11,000 years ago (Flint, 1955) or 18,000 to 24,000 years ago (Hunt 1955, p. 245). Since that time the climate has ameliorated (up to 6,000 to 4,000 years ago), and the present fauna and flora of the region are the result of immigrations from refugia outside the margins of ice-sheets.

There is ample evidence for this amelioration of climate from varied sources. Baker, 1929, noted that from early to late Wisconsin time the number of species of aquatic molluscs in Central America more than doubled. At Minneapolis, Minnesota, the plant fossils in the Mankato soils indicate a forest of White Spruce, *Picea glauca;* Balsam fir, *Abies balsamea*; White Pine, *Pinus strobus;* and birch *Betula* sp., an assemblage of species found today 200 miles north of Minneapolis (Cooper and Foot, 1932). The pollen analysis of peat bogs by Auer, 1930; Deevey, 1939 and 1944; Potzger, 1954; *et al.* all show a general transition in forest species from boreal conifers to mainly deciduous broadleaf trees. Scott (1952) reported the existence of a relict population, presumably from early postglacial times, of Greenland Cod, *Gadus ogac,* in the deep cold water basins of the Bras d'Or Lakes in Cape Breton Island, Nova Scotia. Stephenson (1917) has noted the occurrence of relict arctic environments in the deep fiords of Greenland. Ferguson (1952–53) has discovered species of lepidoptera in Nova Scotia that must be relicts from an earlier colder postglacial period. On pages 172 and 173 he writes "Nova Scotia has no truly alpine conditions, but the presence of many cold, damp sphagnum bogs, as well as exposed, barren headlands along the coast, partly compensates for this deficiency. This close to sea-level it is only in such locations as these that one may still see the last straggling remnants of a Pleistocene fauna that at one time flourished over much of the continent. On the Mount Uniacke Bogs, in association with reindeer moss, crowberry, cloudberry, Labrador tea, and other plants of an Arctic-alpine nature, there exists a very local but seemingly strong colony of *Anomogyna imperita,* which otherwise occurs in the east only in Labrador, northern Quebec, and the high mountains of the Appalachians, around timberline. On these and other bogs fly *Anarta cordigera*, a *Lesionycta* sp., *Syngrapha microgamma, Carsia paludata, Eulype subhastata, Eupithecia gelidata, Oeneis jutta, Lycaeides argyrognomon,* and other distinctly northern species. A stretch of boggy black spruce forest near Parrsboro constitutes the southern-most locality for *Boloria titania* east of the Rocky Mountains."

Pollen analysis, in addition to demonstrating that the climate has ameliorated over the past 18,000 years, also indicates that a warmer and drier climate existed in eastern North America from 6,000 to 4,000 years ago (Flint, 1953, p. 487). Since that time there has been a decided cooling. For example, Potzger (1954) found pollen evidence of a White Pine – broadleaf forest near James Bay, species whose northern limit today lies 350 miles to the south. Auer's work, 1930, in Atlantic Maritime Canada presents a picture of an early postglacial forest of coniferous trees which changed to a deciduous one, and then recently reversed to the present-day transition forest of conifers and broadleafs (The White Pine – Hemlock – Northern Hardwoods forest formation of Nichols, 1935).

Wiseman (1954) has analysed bottom core samples of the equatorial Atlantic Ocean for CO_2 content and concludes that the variations and fluctuations observed are a reflection of the productivity of planktonic Foraminifera. This productivity is, in turn, caused by fluctuations in the surface temperatures of the sea. It follows, then, that the general climate of the world is the ultimate cause of the CO_2 variations in these oceanic bottom samples. Wiseman's figures agree well with those of Arrhenius (1952) for Central Pacific Ocean cores. Wiseman's graph indicates a progressive amelioration from about 13,000 years ago to about 4,000 years ago where the graph levels off and slopes gradually downward, indicating a recent period of cooling. The period of maximum warmth that is evident in the above studies has been termed the Climatic Optimum or Thermal Maximum.

The great significance of this warm period in Eastern Canada is that the various elements of the present flora and fauna must have ranged correspondingly farther north. The subsequent 4,000 years of progressive cooling has forced a southward retreat upon the part of many organisms. However, irregularities in the physiography of North America have made it possible for certain species to survive in a limited area long after they have been forced from the adjacent terrain. This phenomenon of isolated relict populations is a characteristic feature of eastern North America's flora and fauna. Rousseau in his 1951 report to the Arctic Institute of North America (in Montreal) cited the occurrence of large conifers (*Picea mariana* and *Larix laricina*) and even mature White Birch (*Betula papyrifera*) in one of the deep valleys of Labrador near latitude 60°N., which is about 80 miles north of the tree-line and some 150 miles north of the accepted limit of White Birch. Dunbar (1954) notes the occurrence of isolated populations of Eel Grass (*Zostera marina*), the Atlantic Cod (*Gadus callarias*), the copepod (*Acartia clausi*), and the Caplin (*Mallotus villosus*) far north of the continuous range for these species, but attributes this to the mild decade of the 1880's. The present writer believes rather that these populations are at least 4,000 years old. Again, in the southern regions of Nova Scotia, Ferguson (1952–53) collected many "southern" forms of lepidoptera. He remarks on the similarity of this to the many southern species of plants reported by Roland (1944–45) from the same region and goes on to say (p. 176) that "Perhaps at some period a variation in the climate allowed an infiltration of these more southern forms through the Isthmus of Chignecto. Then, in succeeding generations, these populations may have found the extreme southwestern corner of the peninsula most to their liking, taken up their abode there and abandoned the northern isthmus and adjacent area through which they entered." He then lists 24 species to which this might apply.

The isolated populations of amphibians and reptiles in Eastern Canada were described in the discussion of the Herpetofaunal Sections. It can now be seen that they are relicts from the more extensive herpetofauna of the Climatic Optimum period. I suggest that during this warm period the following significant migrations took place (*See* Distribution Maps of species): (1) *Chrysemys picta marginata, Natrix s. sipedon, Hyla v. versicolor,* and *Diadophis punctatis edwardsi* spread northward up the Gatineau Valley; (2) *Clemmys guttata* reached Lake St. Peter on the St. Lawrence River; (3) the forest tree species of the St. Lawrence Valley, and possibly certain amphibians and reptiles, reached Lake St. John via the Saguenay Valley; (4) *Ambystoma jeffersonianum, Rana p. pipiens,* and possibly *Plethoden c. cinereus* and *Hyla c. crucifer,* crossed the mountainous divide between Quebec and southern Labrador and reached the Lake Melville – Hamilton River climatic pocket; (5) *Hyla v. versicolor* and *Desmognathus f. fuscus* spread northward into the St. John River Valley of New Brunswick; (6) *Chrysemys p. picta* and *Chelydra s. serpentina* spread over New Brunswick and Nova Scotia; and (7) *Emys blandingi* and *Thamnophis s. sauritus* came north through New Brunswick, crossed the Isthmus of Chignecto and thence into southern Nova Scotia.

A rather interesting piece of palæo-ecological evidence presents itself in this connection. In Ontario, Quebec, and the New England States, *Lampropeltis doliata triangulum* and *Natrix s. sipedon* range considerably farther north than *Emys blandingi* or *Thamnophis s. sauritus* and therefore, if the same distributional relationship was true about 6,000 years ago, the first two-mentioned species must have arrived at the Isthmus of Chignecto long before the latter two species. Yet it is only *Emys blandingi* and *Thamnophis s. sauritus* which succeeded in crossing over and are now relict in southern Nova Scotia. This means that the selective barrier discussed in the foregoing section on limiting factors may have been functioning in that area some 6,000 years ago.

The origin of the herpetofauna of the large islands in the Gulf of St. Lawrence is an entirely different matter, and it is necessary to consider the postglacial isostatic land movements and ocean level changes. Much of this information and relevant theories are summarized by Flint, 1953. However, some of his data, especially concerning raised beaches and isostatic hinge lines are inaccurate, and I have consulted Dr. V. Prest of the Geological Survey of Canada, Ottawa, and Mr. H. Cameron and Mr. R. MacNeill of the Geology Department of Acadia University, Nova Scotia, for the latest Pleistocene information available on Atlantic Maritime Canada. It seems that this region is only now being studied, and no definite detailed theories can be formulated by the geologists, but they are in agreement over the general sequence of postglacial events in this area.

The paucity of the fauna on Anticosti Island and Newfoundland as compared with the adjacent mainland points to the impossibility of there ever having been a land bridge to these islands in postglacial times. The high incidence of endemism in mammals also points to lack of interchange between island and mainland populations. There is one endemic form on Anticosti Island, and no less than 10 of the 14 mammals on Newfoundland are endemics (A. W. Cameron, Ph.D., thesis 1956, McGill University, Montreal). In contrast, the similarity of the faunas of Prince Edward Island and Cape Breton Island to that of the mainland necessitates the assumption of a postglacial land bridge of some duration. The close taxonomic relationship of the mammalian, amphibian, and reptilian fauna to the mainland has already been discussed in the chapter on factors limiting distribution. Additional evidence of land bridges is the occurrence of six species of strictly fresh-water fishes on Cape Breton Island (Livingstone, 1950–51); of 13 species of fresh-water molluscs on Cape Breton Island (MacMillan, 1953–54); of eight species of fresh-water leeches on Prince Edward Island, six of which must have entered by direct migration, according to Richardson (1943).

Hydrographic maps show 30-mile-long shallows between New Brunswick and Prince Edward Island of from only 30 to 50 feet in depth. There is a 1¾ mile band from Nova Scotia's mainland to Cape Breton Island (in George's Bay) of 90 to 100 feet deep. In contrast, Newfoundland is separated from Labrador by a trough 210 feet deep at the shallowest possible crossing, and Anticosti Island is isolated by 360-foot depths. The geologists whom I have consulted see no objection in postulating a recent land bridge to Prince Edward Island and to Cape Breton Island. The question that geologists cannot answer is precisely when and how these bridges were formed.

After consideration of the known geological facts and of the faunal distribution patterns, the following analysis of postglacial events is suggested. It is well known that the weight of the glacial age depressed the land to the extent that since the ice retreated, upwarping has amounted to 1,000 feet in parts of Ontario. However, in Nova Scotia, which was near the periphery of the ice-sheets, there was little change in the level of the land, and a zero hinge line (where there is no upwarping) extends through the centre of the province in northwest-southwest direction (Flint, 1953, pp. 420 and 426). Studies of strand line west of this zero hinge line reveal that upwarping varied from 75 feet on Prince Edward Island to 90 feet in parts of western Nova Scotia. At the same time, the sea-level at the peak of the glaciation (18,000 years ago) was 230 to 330 feet below its present level but with the melting of the glaciers it has risen correspondingly (Flint 1953, p. 427). The sea rose faster than the land, and it is this time lag in the upwarping of the land that accounts for strand lines at altitudes of 90 feet. I have diagrammed these events (Diagram 1) and their relationships to the land bridges. At maximum glaciation the land of western Nova Scotia and Prince Edward Island was depressed 85 feet and the sea 250 feet, but near the strait of Canso the land depression figure was nearly zero. Therefore, at Northumberland Stait the present-day 40-foot-deep channel was depressed another 85 feet, making it 125 feet below present sea-level. In contrast, the Strait of Canso was depressed possibly but 10 feet giving it a total depression of only 100 feet. It follows, then, that with the melting of the glacial ice over this area, probably early in postglacial times, because it was thinner older ice and at the southern margin of the ice sheet (possibly about 15,000 to 14,000 years ago during the retreat of the Cary and before the advance of the Mankato; Manley, 1955, and Flint, 1955) the bridge to Prince Edward Island would flood before the Canso one, in spite of the former being the shallower of the two straits at the present day. To flood the Prince Edward Island land bridge would necessitate a rise of 125 feet in sea-level, which is about one-half of the total lowering of sea-level during the last glaciation. This means that nearly one-half of the glacial ice must have melted, and it follows that at this stage of deglaciation the climate of the peripheral area such as New Brunswick, Prince Edward Island, and Nova Scotia must have been rather mild. Therefore, the period between the retreat of the ice from New Brunswick, Nova Scotia, and Prince Edward Island, and the flooding of the dry bridge is the only period in which the flora and fauna could have entered Prince Edward Island directly and en masse.

The flora and fauna must have followed on the heels of the glaciers, and the climate must have been mild to account for such a rich fauna and flora having crossed the land bridge so early in postglacial times.

In this connection the distribution of many fresh-water fishes shows that they must have utilized streams formed from glacial melt-water to cross over watersheds which are now unconnected (Radforth, 1944). Coleman (1922) points out that all the molluscs known from deposits of Lake Agassiz are still living in Lake Winnipeg. Deevey (1949, p. 1394), sums up this evidence by saying "At present it can only be pointed out that modern distribution patterns of aquatic forms in general agree with the fossil evidence that parts of the great glacial lakes, though no doubt colder than their descendants today, were definitely not arctic.... A subarctic tundra zone must have followed the retreating ice from across the northern United States and Canada ... but the tundra must have been very narrow and impermanent, and the modern flora and fauna immigrated astonishingly early." From herpetofaunal evidence it is apparent that the early postglacial climate of the Atlantic Provinces must have been mild enough to support all the present species now in the area except the turtles, the Bull Frog, *Rana catesbeiana,* and possibly the Ring-necked Snake, *Diadophis punctatus edwardsi,* which are, fittingly enough, the most southerly elements of the present herpetofauna in that region. By the time the climate was propitious for these forms, the land bridge to Prince Edward Island was submerged. The bridge to Cape Breton Island probably was submerged a few thousand years later, but the turtles and R. *catesbeiana* and *D. punctatus edwardsi* did not reach it (for unknown reasons, but possibly because of a local cold influence from the Atlantic Ocean). The four mammals, Woodchuck, Raccoon, Porcupine, and Striped Skunk, also missed both these land bridges, though temperature was probably not the delaying factor in their case.

Strictly freshwater fish, which must cross watershed divides in order to get from one drainage system to another, migrate more slowly than the terrestrial amphibians and reptiles. They apparently arrived in eastern New Brunswick after the land bridge to Prince Edward Island had been flooded and are absent from that island (pers. comm. with W. Saunders of Ellerslie Biological Station, and personal field work in that province). However, 12 species migrated into Nova Scotia, and six of these reached Cape Breton Island before the land bridge to that island became submerged.

There has been some speculation by botanists (especially Fernald, 1918, 1921, and 1924) of the possibility of plants having entered Nova Scotia via a land connection from Cape Cod. If the sea had been lowered 300 feet by the formation of the glaciers, then the Brown's Bank would be exposed forming an island between Nova Scotia and Cape Cod, with saltwater gaps of 28 and 19 miles on either side. These gaps would be a formidable barrier for the amphibians and reptiles (in the opinion of this writer), the freshwater fish (Livingston 1950-51, p. 8), and the Lepidoptera (Ferguson, 1951–53, p. 176) to cross, although certain plants could possibly do it. A drop in sea-level of 900 feet would be required to form a continuous bridge from New England to southern Nova Scotia. If such a bridge had existed, one would expect many more species of reptiles (and other organisms) to be relict in southern Nova Scotia. More in keeping with the evidence is the hypothesis that they travelled north through Maine and New Brunswick, crossed at the Isthmus of Chignecto, and came south again through the Nova Scotia peninsula.

The British Isles were subjected to a glacial and postglacial history similar to that of Eastern Canada, and so it is of interest to compare the history of the herpetofauna of those islands as reported by Smith (1951). During the last glacial epoch the south of England was not glaciated, and it is possible that three species, *Rana t. temporaria, Vipera b. berus,* and *Lacerta vivipara,* which today live within the Arctic Circle, survived that epoch. When the glaciers began retreating some 15,000 to 12,000 years ago, the British Isles were an integral part of Europe, and the European species of amphibians and reptiles began their invasion of that peninsula. However, as the ice melted, the sea-level rose, and about 7,000 years ago (Stamp, 1946) the Straits of Dover were formed. There was, then, but 5,000 to 8,000 years during which migrations could take place over the land bridge. Six amphibians and seven reptiles invaded the British Isles, but since the northern half of the area was depressed from 25 to 100 feet (Wright, 1937, and Zenner, 1938), it flooded first and consequently cut off the direct migration routes to the numerous islands early in postglacial times. Only two species, *Lacerta vivipara* and *Triturus v. vulgaris,* managed to reach Ireland; only *Bufo b. bufo* reached Orkney; and *Anguis fragilis* is the sole representative of the herpetofauna in the Outer Hebrides. The limited herpetofaunas of these islands, each with a different species, strongly suggest chance introduction across water. The climate of England some 5,000 years ago was apparently much warmer and drier, for the European Pond Turtle, *Emys orbicularis,* was one of the seven reptilian immigrants, as is evident from their remains found in peat bogs in southern England. This period would coincide with the Climatic Optimum. However, with an increasingly cooler and damper climate over the past 5,000 years, this turtle became extinct in England and in northern Europe and is today found only in central and southern Europe where the more continental climate is propitious for the successful development of its eggs (Rollinet, 1934). This brief account shows similarities to the postglacial history on the Canadian side of the Atlantic Ocean on the following points: (1) There is evidence in both areas of land bridges which were flooded by a rise in sea-level, and thus the direct immigration of certain species was prevented. (2) Hinge lines and land depression, owing to the weight of glacial ice and time lag in unwarping, explain the differential flooding of these land bridges. (3) The relict populations of reptiles, particularly *Emys blandingi* in southern Nova Scotia and New England, and the remains of *Emys orbicularis* found in England and in northern Europe, necessitate the occurrence of a warm period (Climatic Optimum) to explain such a zoogeographic sequence.

Another aspect of the history of the postglacial herpetofauna of Eastern Canada to be considered is the several apparent routes of immigration employed by these species. These routes are best understood by first pointing out the postglacial centres of dispersal that existed in early postglacial times. Adams (1902) and Brown (1904) have summarized both floral and faunal evidence, which points to the southeastern United States (the Georgia – Florida – Mississippi area) and the southwestern United States (the Texas – Arizona – Mexico area) as the two centres from which postglacial emigration took place. Species from the first-mentioned centre are primarily inhabitants of moist forested regions, whereas the species from the southwest centre are for the most part inhabitants of arid grassland regions. They have dispersed from their respective centres, and now the ranges of many of them merge along a corridor between longitude 96°W. and 98° W., which corresponds roughly with the grassland-forest ecotone.

Brown's 1904 analysis of the reptilian genera traces them back to their respective centres of origin, and he concludes that turtles and snakes were the dominant forms in the southeast refuge and that lizards must have predominated at the refuge in the Mexico area. More recently, Chapman, 1936 and 1940, has illustrated this dicentric pattern through his analysis of the three subspecies of the grackle, *Quiscalus quiscala,* showing that Pleistocene isolation in refuges in Florida and Mexico is clearly evident.

There is additional evidence that the southeastern United States should be subdivided into several smaller refugia. Adams (1902, p. 129) lists the Mississippi Valley, the Atlantic Coastal Plain, and the Appalachian Mountains as the three primary outlets of dispersal from the southeast. However, Brown (1904, p. 474) implies that one of these may not have been only an avenue of dispersal but may well have been a secondary refuge, for he says "The lower Mississippi Valley may indeed, with some reason, be regarded as a secondary and more modern center of development in Chelonia and Ophidia." Halliday and Brown (1943) have expressed the belief that Red Spruce, *Picea rubra,* and Balsam Fir, *Abies balsamea,* survived glaciation on the Atlantic Coastal Plain; that Jack Pine, *Pinus banksiana,* had refugia both on the Atlantic Coastal Plain and in Wisconsin; and that Yellow Birch, *Betula lutea,* was isolated in Wisconsin, the Appalachian Mountains, and on the Atlantic Coastal Plain. Deevey (1949, p. 1392) discussed the distribution of the three subspecies of the Johnny Darter, *Boleosoma nigrum,* and concludes that the last glaciation split the parent population of this species so that one segment survived in western Wisconsin, one in the Mississippi Valley, and one on the Atlantic Coastal Plain. A triple division of the turtle genus, *Gopherus,* is evident on the map in Carr's book (1952). There is a species near the west coast, a second in southern Texas, and a third in the southeastern region of the United States. The ranges of these three forms are not now in contact.

These selected examples should suffice as evidence for assuming a series of refugia across southern North America at the height of glaciation. From the new information presented here on the distribution of many species, it is now possible to postulate with some assurance the immigration route of these forms into Canada. There seem to have been four main avenues of dispersal from the south which have contributed to Canada's eastern hepetofauna, namely (1) the southwest prairies; (2) the Mississippi and tributary valleys; (3) the Appalachian Mountains; and (4) the Atlantic Coastal Plain. The species which can be traced back to these four centres of dispersal are listed accordingly in Table 4, and the accompanying maps show the pattern of dispersal for each group.

Those species having affinities with the western prairies have gained entrance to eastern North America via the now extinct Prairie Peninsula, which in early postglacial times extended eastward south of the coniferous forest and north of the deciduous vegetation as far as Ohio and Pennsylvania. Transeau, 1935, summarized the botanical evidence for this peninsula. Schmidt, 1938, has discussed the species of amphibians and reptiles whose distribution patterns correspond to this prairie tongue. Some of these species are prairie peninsula endemics, namely *Thamnophis butleri, Sistrurus c. catenatus, Natrix kirklandi,* and *Elaphe vulpina gloydi,* but are taxonomically related to midwestern forms. There are other species whose main range is in the midwest, but an eastern distributional tongue is plainly evident, although in some cases it is now broken up into isolated relict populations. *Terrapene o. ornata, Coluber constrictor flaviventris, Pseudacris nigrita triseriata* (listed only tentatively by Schmidt), and *Kinosternon flavescens* (not included by Schmidt) represent these cases. I cannot agree with Schmidt's inclusion of *Chrysemys picta marginata,* for it is obviously an endemic of the Mississippi and tributaries, having occupied southern Ontario and Quebec as well as the Prairie Peninsula States and having crossed the Appalachian Mountains to form a broad band of intergrades with *Chrysemys p. picta* of the Atlantic Coastal Plain. This extensive eastern distribution pattern is not at all typical of Prairie Peninsula species. Bishop and Schmidt (1931, p. 137) state that *Chrysemys picta dorsalis* of the lower Mississippi Valley is easily derived from *Chrysemys picta marginata,* which further ties *Chrysemys picta marginata* to the Mississippi Valley refugium and leaves the prairies and western margin of the eastern forest to *Chrysemys picta belli.* Schmidt's inclusion of *Emys blandingi* is also unwarranted, for it has no midwestern affinities and occurs in the New England States and in Nova Scotia. In contrast, few of the true Prairie Peninsula forms have spread farther east than Lake Ontario, and only *Pseudacris nigrita triseriata* has extended its tongue pattern of distribution as far as southern Quebec, and this is probably due to the artificial creation of small tracts of grassland through farming.

Only four species that enter southern Canada can be assigned to the postglacial dispersal route of the Mississippi Valley and tributaries, and thence into the Great Lakes and the St. Lawrence River system. They are *Necturus m. maculosus, Chrysemys picta marginata, Trionyx ferox spinifera,* and *Graptemys geographica,* and as the distribution pattern of *Necturus m. maculosus* admirably shows, several have subsequently migrated along some of the larger valleys of the Appalachian range (Richelieu-Hudson rivers, Oswega-Susquehanna rivers, and Oswega-Delaware rivers) and reached the Atlantic coast watershed.

It seems reasonable to assume that the southern Appalachian Mountains served as the refuge for the plethodontid salamanders, particularly the stream forms. Since the mountains would be the last area to deglaciate, one would not expect these stream salamanders to have penetrated very far into Canada. Such is the case with *Eurycea b. bislineata, Gyrinophilus p. porphyriticus,* and *Desmognathus f. fuscus,* which have dispersed both east and west from the Appalachian chain but not into Canada to the extent of most other amphibians. The distribution pattern of the bog-meadow turtle *Clemmys muhlenbergi* is also centered on the Appalachian Mountains. Carr's map (1952) shows it at the border near Niagara, but it has not been recorded from the Canadian side.

The following group of reptiles must have survived glaciation in the Atlantic Coastal Plain refuge: *Chrysemys p. picta, Emys blandingi, Clemmys insculpta,* and *Clemmys guttata.* Their distribution patterns are similar to that of the Johnny Darter subspecies, *Boleosoma nigrum olmstedi,* also isolated on the Atlantic Coastal Plain during glaciation. They have migrated northward along the coast into Maine and (except for *C. guttata*) into maritime Canada, have crossed the Appalachians via the Hudson, Susquehanna, and Delaware river valleys, and extended their ranges westward through Ontario via the Great Lakes.

It is apparent from the foregoing that the "southern" or warmth-loving species, mainly reptiles, are the forms whose distribution patterns illustrate their postglacial avenues of dispersal. This is only reasonable because the boreal elements of Canada's herpetofauna (i.e. most of the frogs, tree frogs, salamanders, and the cold-tolerant reptiles) followed close behind the retreat of the glaciers, and have been extending and overlapping their ranges for a considerably longer time than the more southern species. Perhaps future detailed taxonomic studies of these species will reveal evidence of an ancient dicentric origin. It is more probable, in this writer's opinion, that the boreal frogs, tree frogs, salamanders, and reptiles survived glaciation in the lakes, bogs, and streams of the southern Appalachian Mountains; hence their dispersal has been east, west, and north from this range rather than a dicentric dispersal paralleling the mountains. In such a case no specific dispersal route would be evident at this late date of the postglacial period. These eastern Canadian species which today are distributed generally throughout the eastern forested regions of North America are listed in Table 5.

This discussion of dispersal routes is of significance to the taxonomist, emphasizing as it does the dynamic nature of the taxonomy of organisms in North America. A similar situation may apply in Europe where glaciation split parent populations and forced them southwestward into Spain and southeastward into the Asia Minor region. As is evident from the few examples given, the species and subspecies of many recent forms were not derived from a single parent population, as is commonly assumed to be the case, but were derived from as many as three isolated parent populations located in the refuges across southern United States 18,000 to 20,000 years ago. What were full species (in the sense of reproductively isolated populations) some 20,000 years ago may now be subspecies, races, or may even form a bewildering complex of intermediate types. The taxonomist would be wise not to create new trinomials or binomials without first considering the distribution pattern of the genus and species with which he is working and deciphering the postglacial dispersal route or routes of the group. The true systematic relationship of two samples might thus be found by first solving the relationship of each population to the various postglacial route. Through this realistic approach one can distinguish between (1) intermediate forms resulting from clinal differentiation within one dispersal route, which would be differentiation within the stock from a single postglacial parent population; and (2) intermediate forms resulting from contact between populations of slightly differentiated individuals from two or more dispersal routes, which would be a form of hybridization between stocks from two or more postglacial parent populations.

UNSOLVED PROBLEMS

Many interesting problems have come to light during the progress of this survey, and some of them are outlined here in the hope that other persons may feel stimulated to investigate a few of them.

1. It would be of immense value to students of zoogeography and ecology to know what the limits of tolerance are for each species of amphibian and reptile in relation to the various environmental factors and at each stage of the species life-history. There is no end to the laboratory and field work that can be done in this connection. Studies in Canada would be of particular interest, for it is here in northern latitudes that such phenomena as the overwintering of turtle eggs in the nest and the overwintering of frog and salamander larvæ are of widespread occurrence.
2. Most species of amphibians and reptiles become more rare in numbers of individuals at the periphery of their range, but *Pseudacris nigrita triseriata* is an exception in Canada. This is particularly evident in southeastern Quebec where by driving over the network of roads in the Eastern Townships it is possible to draw a line that marks the edge of this species' range. The range has a tongue shape in this area. Within the tongue, during the spring breeding season, this species is abundant and can be heard in nearly every pond and ditch. Why the population density of this frog changes directly from abundant to zero along this line would make an interesting problem in factors limiting distribution.
3. It is the cold-tolerant amphibians which breed in early spring that range the farthest north, but there are exceptions. *Ambystoma maculatum* and *A. jeffersonianum* both breed when the ice first leaves the ponds and ditches, yet the latter species ranges more than 100 miles farther north than A. *maculatum*. Again, *Pseudacris nigrita triseriata* is the first anuran in Ontario to begin calling in spring. It may even come out of hibernation before *Rana sylvatica*, which ranges northward to the tree-line, yet *P. n. triseriata* has the least extensive range of any frog in Eastern Canada. Even *Rana catesbeiana*, which breeds in June to July, ranges farther north.
4. There is the problem of what controls the population densities of frogs and salamanders that inhabit areas where there is an abundance of ponds and insect prey, as in northern Quebec and Labrador, but where their natural predators, such as snakes, bull-frogs, turtles, skunks, and raccoons are absent. Amphibians may in fact even be quite rare in such a seemingly ideal situation.
5. In northern Quebec and Labrador the problem arises of how and where the frogs hibernate in a terrain of rock and permafrost. Bog and pond bottoms seem to be the logical site, but it would be of value to verify this and to have precise measurements of thickness of ice, water temperatures, and temperature data of the bottom ooze in which the frogs hibernate.

6. A physiological problem at the ordinal level is, why do salamander larvae and adults remain active (or semi-active) during winter even beneath ice, while frogs and tadpoles become inactive at such temperatures. But note that it is the frogs and not the salamanders that range north to the tree-line.
7. Various north-south and east-west clines in colour and structure have been recorded for amphibians and reptiles, but the physiological basis for these changes are unknown.
8. During the spring breeding season of anurans they become concentrated in vast numbers at very limited sites, such as a pond, a lake shore, a ditch, and present a conspicuous and rich (in numbers) source of food. One would think that nocturnal predators of all kinds would descend upon such a larder, but no study with this objective in mind seems to have been attempted.

SUMMARY

During the period May 1950 to July 1956 the writer collected specimens of amphibians and reptiles from many parts of Eastern Canada. All of the sites visited are plotted on Map 1. The area of zoogeographic study includes eastern Ontario, Quebec, Labrador, Newfoundland, New Brunswick, Prince Edward Island, and Nova Scotia. In addition faunal peculiarities west and south of this area are occasionally referred to. Over 6,000 specimens comprising 34 species were collected, and these were deposited with the Nova Scotia Museum of Science and the National Museum of Canada.

The author's records and all available previous reports are plotted on spot distribution maps for 43 species. The ranges of 30 of these species were extended through the author's field collecting. With these records and the author's field notes, the herpetofauna of Eastern Canada is analysed and shown to consist of 16 distinct Herpetofaunal Sections, based on differences in species composition and population densities. Several of these sections are characterized by relict populations from the Climatic Optimum Period of 6,000 to 4,000 years ago. Wherever possible, reference has been made to examples of flora, invertebrates, and vertebrates other than amphibians and reptiles which add supporting evidence to the zoogeographic picture. The richest herpetofauna occurs west of the Appalachian Mountains in eastern Ontario, maritime Canada east of the Appalachians has the second most species, and Quebec province north of the St. Lawrence Lowlands and Labrador have the least numbers of species.

The variations in temperature and topography in Eastern Canada strongly influence the distribution of the amphibians and reptiles. These factors and others which seemingly limit dispersal are discussed. An Environmental Temperature Index is derived from meteorological data and when plotted is found to fit the contours of the Herpetofaunal Sections remarkably well.

The postglacial immigration of amphibians and reptiles into Eastern Canada is discussed. The postglacial isostatic land movements and changes in sea-level are correlated with the faunas of the islands of the Gulf of St. Lawrence. It is concluded that Newfoundland and Anticosti Island, which have unbalanced faunas, were never connected to the mainland, and

that Cape Breton Island and Prince Edward Island, which possess relatively complete faunas, were connected by ice-free land bridges to the adjacent mainland some 16,000 to 10,000 years ago. A comparison is made with the postglacial sequence of the herpetofauna of Ireland, Britain, and adjacent parts of Europe.

Evidence is given for the existence of several distinct refugia at the time of maximum glaciation along the southern boundary of what is now United States. Many of the eastern Canadian amphibians and reptiles are traced back to their original centres of dispersal, which are (1) the Mexico-Texas area, (2) the lower Mississippi Valley, (3) the southern Appalachian Mountains, and (4) the Atlantic Coastal Plain. Their dispersal patterns from these centres are discussed and mapped.

From the aspect of taxonomy, it is important to realize that taxonomy in North America is a dynamic thing and always relative to early postglacial times when there existed as many as three isolated parent populations of a single species.

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Table 1.—Relative abundance of amphibian species in different areas of Eastern Canada

Amphibians	southcentral Nova Scotia	Annapolis Valley, Nova Scotia	Musquodoboit and Gay R. Valleys	Oxford, N.S.	Cape Breton Island	Cape Breton Island Plateau	Prince Edward Island	southcentral New Brunswick	northern New Brunswick	Gaspe Peninsula, Quebec	Anticosti Island	Newfoundland	eastern Ontario	Gatineau Valley	St. Lawrence Lowlands	southeastern Quebec	southern Laurentian Mts.	Saguenay Valley, Lake St. John	North Shore of Gulf St. Lawrence	Lake Melville, Labrador	Knob Lake, Menihek Lake	Ungava to the Tree-line
Necturus maculosus maculosus													C	–	C	–	–					
Ambystoma jeffersonianum	C	?	?	?	–	–	R	C	C	C			C	C	C	C	C	C	C	R	–	–
Ambystoma maculatum	C	C	C	C	C	?	C	C	C	C			C	C	C	C	?	–	–	–	–	–
Diemictylus v. viridescens	C	C	C	C	C	A	A	C	C	C			C	C	C	C	C	–	–	–	–	–
Desmognathus fuscus fuscus	–	–	–	–	–	–	–	C	–	–			–	–	–	A	–	–	–	–	–	–
Plethodon cinereus cinereus	C	C	C	C	C	C	R	C	C	C			C	C	C	C	C	R	R	?	–	–
Hemidactylium scutatum	R	R	–	–	R	–	–	–	–	–			C	R	–	–	–	–	–	–	–	–
Gyrinophilus p. porphyriticus													?	–	–	C	–	–	–	–	–	–
Eurycea b. bislineata	–	–	–	–	–	–	–	C	R	C			A	C	?	A	C	C	R	–	–	–
Bufo americanus	C	A	C	C	C	?	C	C	C	C			C	C	C	C	C	C	C	C	R	–
Hyla crucifer crucifer	C	C	C	C	C	?	C	C	C	C			C	C	C	C	C	C	R	?	?	–
Hyla versicolor versicolor	–	–	–	–	–	–	–	R	–	–			C	C	C	–	–	–	–	–	–	–
Pseudacris nigrita triseriata													C	R	C	–	–	–	–	–	–	–
Rana catesbeiana	A	C	?	C	–	–	–	C	–	C			C	C	C	R	C	–	–	–	–	–
Rana clamitans	C	C	C	C	C	C	A	C	C	C	–	C	C	C	C	C	C	?	R	–	–	–
Rana septentrionalis	C	C	C	C	C	?	?	C	C	C	C	–	R	C	R	C	C	C	C	R	R	R
Rana sylvatica	C	C	C	C	C	?	C	C	C	C			C	C	C	C	C	C	C	C	R	R
Rana pipiens pipiens	C	C	C	C	C	?	C	C	C	C	C	–	C	C	C	C	C	C	R	C	–	–
Rana palustris	A	C	C	C	C	?	?	C	C	C			C	R	?	C	R	–	–	–	–	–

A=abundant. C=common. R=rare. –=absent. ?=insufficient data.

Table 2.—Relative abundance of reptile species in different areas of Eastern Canada

Reptiles	southcentral Nova Scotia	Annapolis Valley, Nova Scotia	Musquodoboit and Gay R. Valleys	Oxford, N.S.	Cape Breton Island	Cape Breton Island Plateau	Prince Edward Island	southcentral New Brunswick	northern New Brunswick	Gaspe Peninsula, Quebec	Atlantic Ocean, Nova Scotia	Atlantic Ocean, Newfoundland	eastern Ontario	Gatineau Valley	St. Lawrence Lowlands	southeastern Quebec	southern Laurentian Mts.	Saguenay Valley, Lake St. John	North Shore of Gulf St. Lawrence	Lake Melville, Labrador	Knob Lake, Menihek Lake	Ungava to the Tree-line
Chelydra s. serpentina	A	R	R	R	–	–	–	R	–	–			C	C	C?	R	R	–	–			
Sternotherus odoratus													R	–	–	–	–	–	–			
Clemmys guttata													–	–	?	–	–	–	–			
Clemmys insculpta	–	R	C	C	–	–	–	C	R	–			C	C	C	R	R	–	–			
Emys blandingi	R	–	–	–	–	–	–	–	–	–			C	–	–	–	–	–	–			
Graptemys geographica													C	–	R?	R	–	–	–			
Chrysemys picta picta	A	C	C	R	–	–	–	R	–	–												
Chrysemys picta marginata													A	R	C	–	–	–	–			
Lepidochelys olivacea kempi											R	?										
Caretta caretta caretta											R	R										
Dermochelys coriacea coriacea											R	R										
Trionyx ferox spinifera													R	–	R	–	–	–	–			
Eumeces fasciatus													R	–	–	–	–	–	–			
Natrix sipedon sipedon													C	C	R	–	R	–	–			
Storeria dekayi dekayi													R	–	C	–	–	–	–			
Storeria o. occipitomaculata	C	C	C	R	R	–	C	C	R	–			C	C	C	C	?	–	–			
Thamnophis sauritus sauritus	R	–	–	–	–	–	–	–	–	–			R	–	–	–	–	–	–			
Thamnophis sirtalis sirtalis	A	C	C	C	C	R	R	C	R	R			A	C	C	C	C	R	R			
Diadophis punctatus edwardsi	C	R	R	R	?	?	?	R	R	–			R	R	R	R	R	–	–			
Opheodrys v. vernalis	C	C	C	R	R	R	R	R	R	–			C	C	C	?	R	–	–			
Coluber constrictor constrictor	?	?				?	?	?														
Elaphe vulpina gloydi													?									
Elaphe obsoleta obsoleta													R									
Lampropeltis doliata triangulum													C	R	R	R	–	–	–			

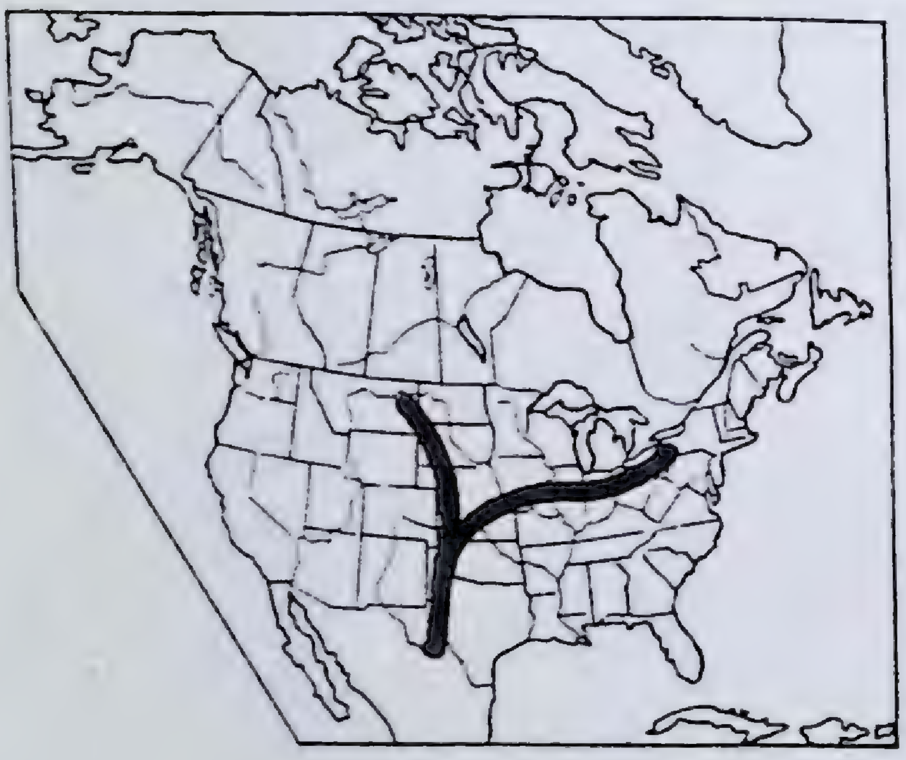
A=abundant. C=common. R=rare. —=absent. ?=insufficient data.

Table 3.—Numerical distribution of the species of amphibians and reptiles of Eastern Canada within the Herpetofaunal Sections

Herpetofaunal Section Numbers	No. of Species		Total
	Amphibians	Reptiles	
1	18	17	35
2 (west of Appalachians)	19	13	32
3	15	7	22
2A (N.S.)	13	9	22
3A (N.S.) (east of Appalachians)	13	7	20
2A (N.B.)	15	7	22
3A (N.B.)	13	5	18
D3A (C.B.I.)	12	3	15
D3A (P.E.I.) (Gulf Islands)	12	3	15
D3A (Newfoundland)	1	—	1
D3 (Anticosti)	2	—	2
4	10	1	11
4A (northern and montane regions)	12	1	13
5	9	1	10
5A	6	—	6
6	3	—	3
7	2	—	2

Table 4.—Refuges during maximum glaciation and Eastern Canadian species which came from them

(1) *Mexico-Texas Area*
- Pseudacris nigrita triseriata
- Thamnophis butleri
- Elaphe vulpina gloydi
- Coluber constrictor flaviventris
- Sistrurus catenatus catenatus



(2) *Lower Mississippi Area*
- Necturus maculosus maculosus
- Chrysemys picta marginata
- Trionyx ferox spinifera
- Graptemys geographica

(3) *Southern Appalachian Mountains*
- Desmognathus fuscus fuscus
- Gyrinophilus porphyriticus porphyriticus
- Eurycea bislineata bislineata
- Clemmys muhlenbergi

(4) *Atlantic Coastal Plain*
- Chrysemys picta picta
- Emys blandingi
- Clemmys guttata
- Clemmys insculpta

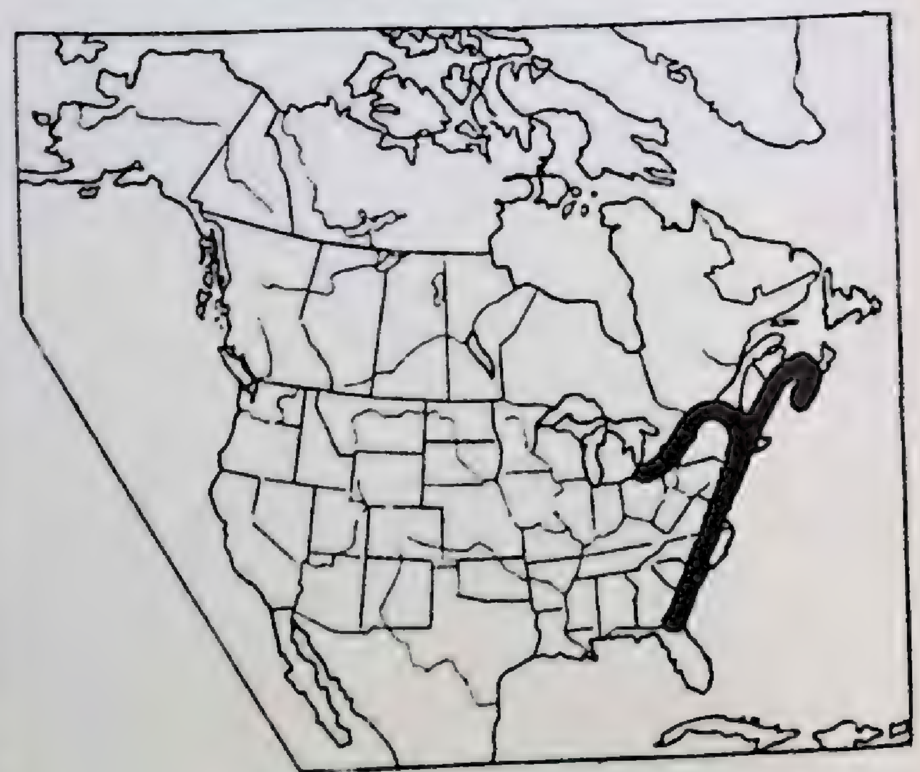


Table 5.—Eastern Canadian species which are distributed generally over much of eastern North America

Amphibians	*Reptiles*
Diemictylus viridescens viridescens	Chelydra serpentina serpentina
Ambystoma jeffersonianum	Sternotherus odoratus
Ambystoma maculatum	Eumeces fasciatus
Plethodon cinereus cinereus	Natrix sipedon sipedon
Hemidactylium scutatum	Thamnophis sauritus sauritus
Bufo americanus	Thamnophis sirtalis sirtalis
Hyla versicolor versicolor	Storeria occipitomaculata occipitomaculata
Hyla crucifer crucifer	Diadophis punctatus edwardsi
Rana catesbeiana	Opheodrys vernalis vernalis
Rana clamitans	Elaphe obsoleta obsoleta
Rana septentrionalis	Coluber constrictor constrictor
Rana sylvatica	Lampropeltis doliata triangulum
Rana pipiens	
Rana palustris	

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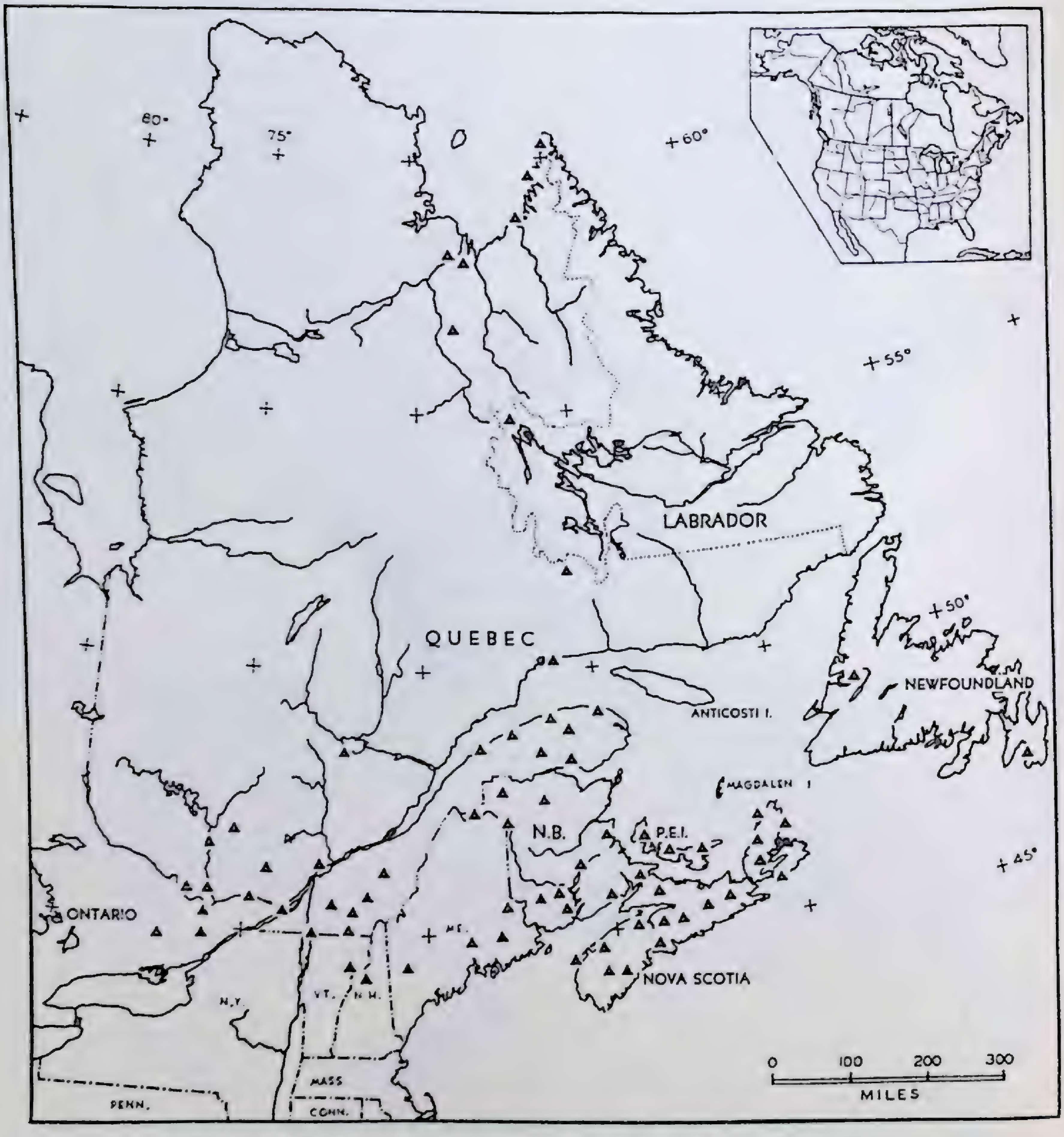
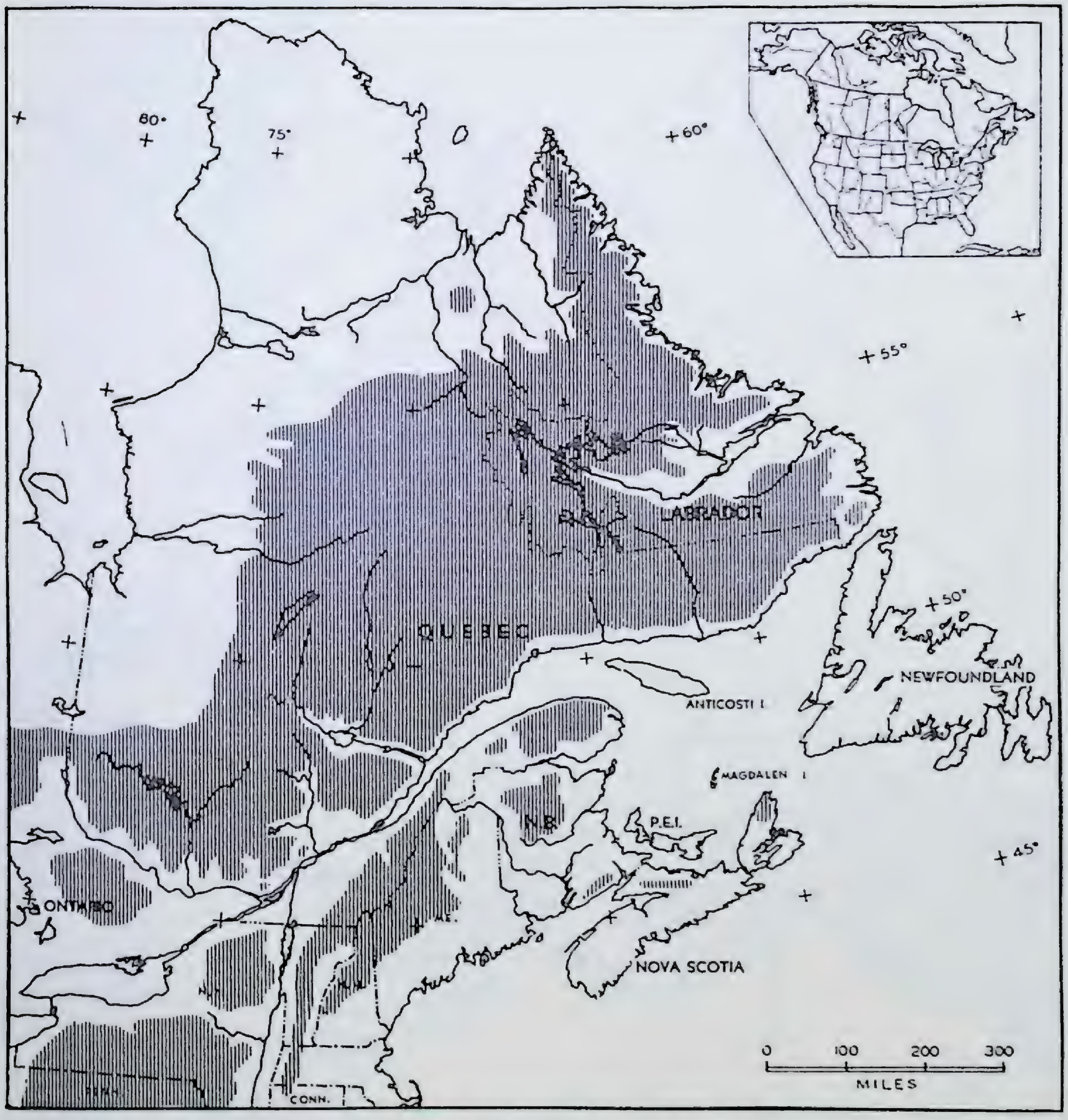


MAP 1. Black triangles represent sites visited by the author.



MAP 2. Areas in Eastern Canada and New England over 1,000 feet in altitude.

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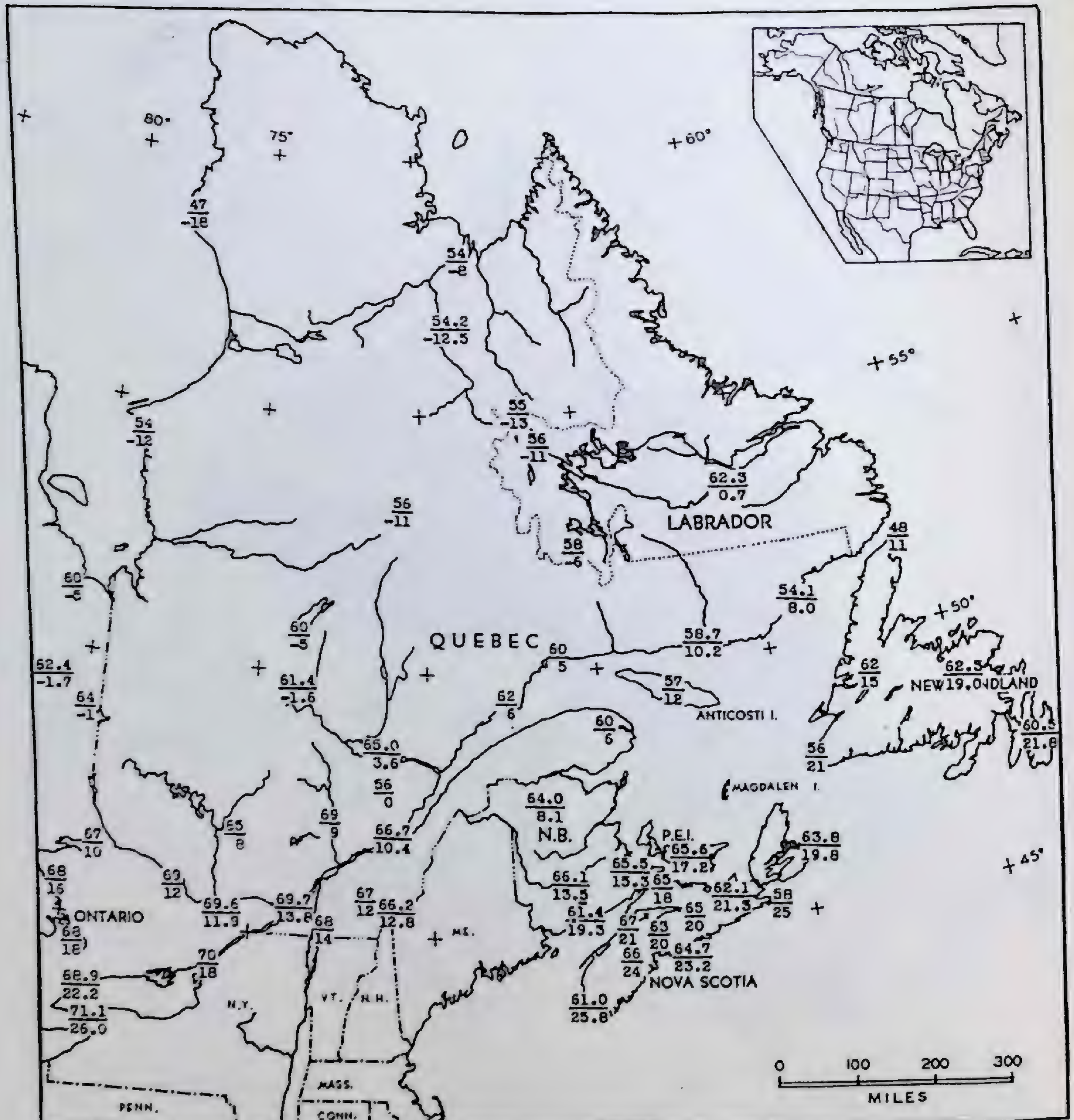
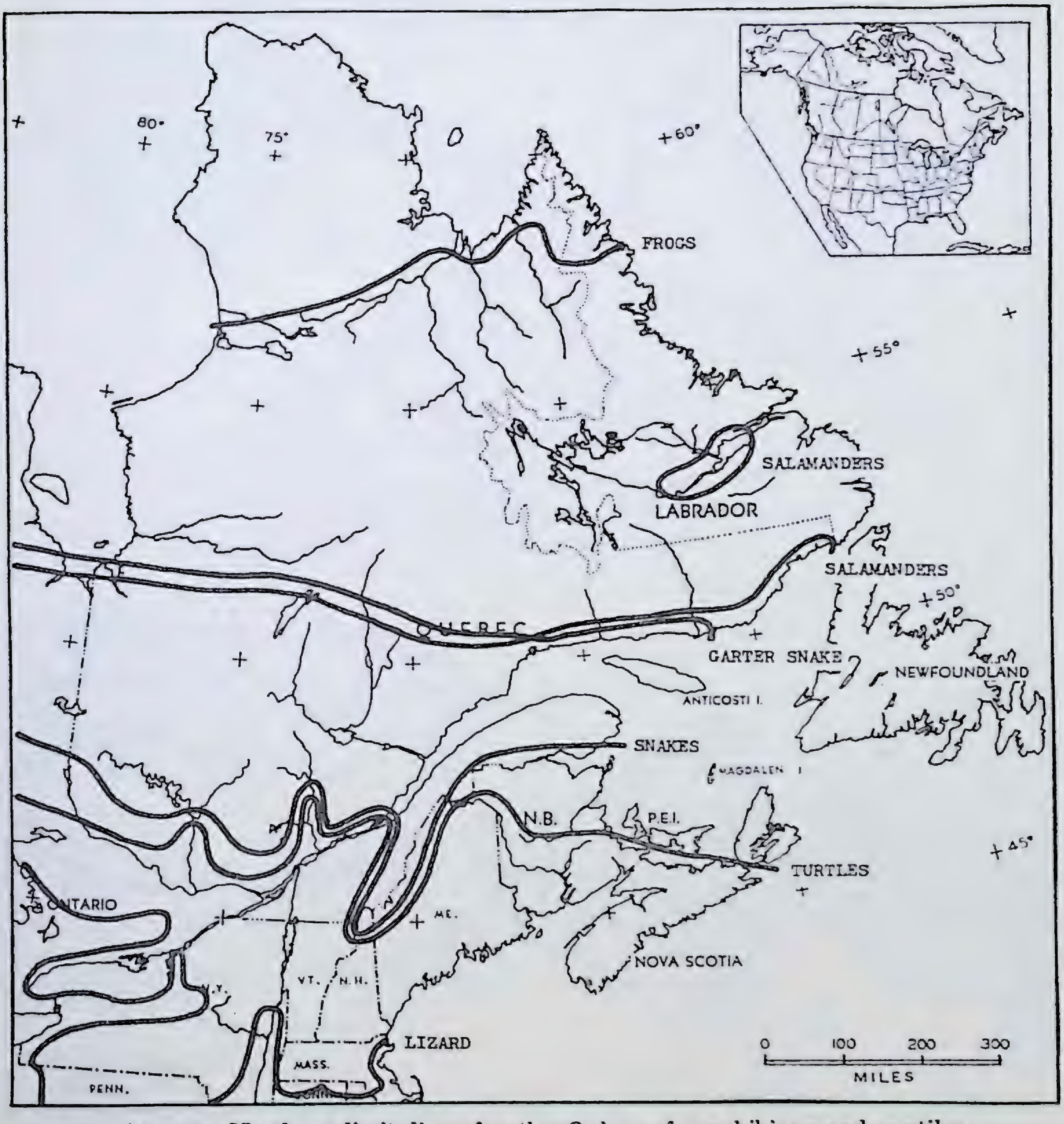


Map 3. Mean temperature of warmest month over mean temperature of coldest month.

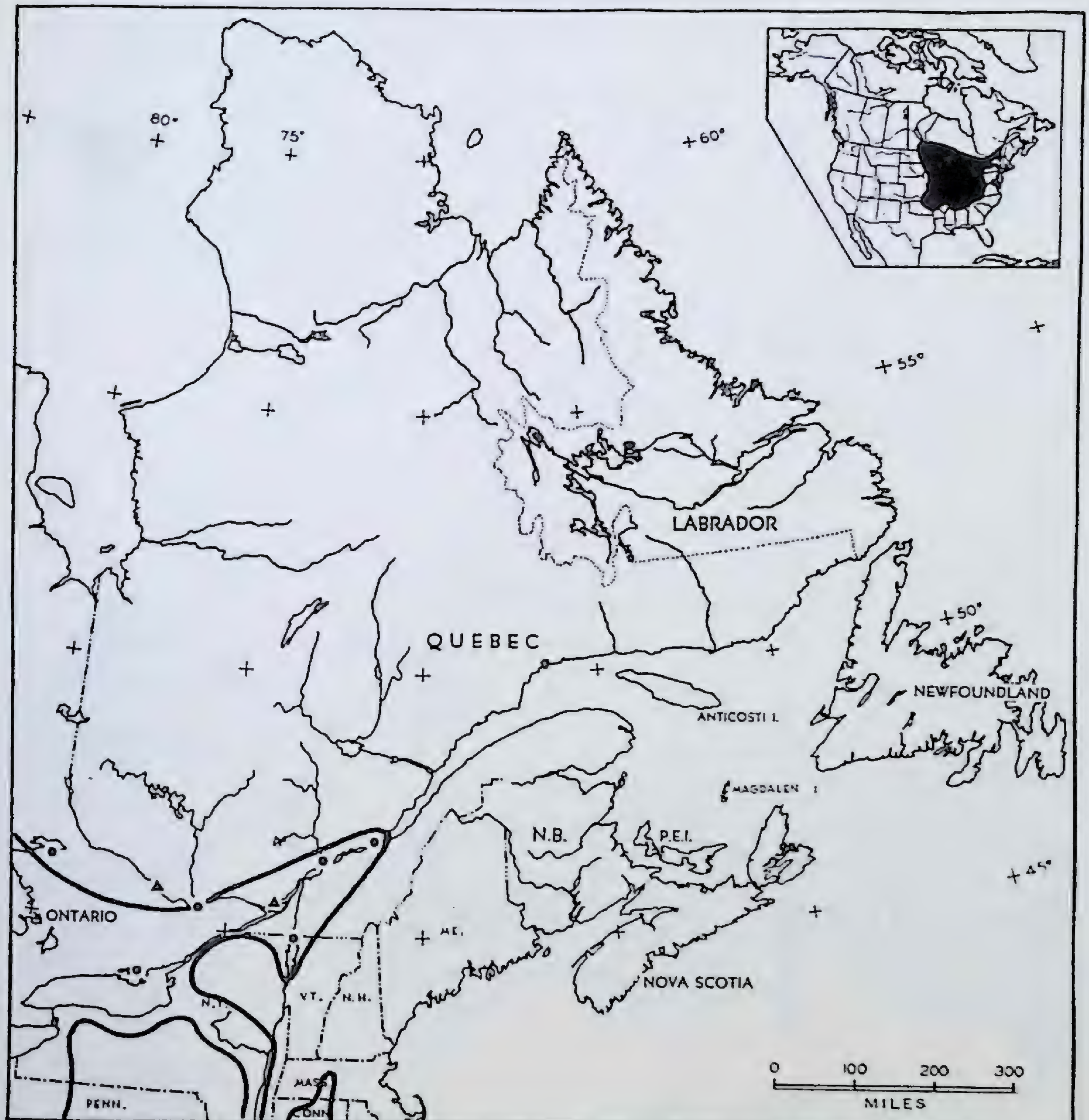
MAP 4. Solid lines delineate the four major forest formations in Eastern Canada: Deciduous Forest; Great Lakes – St. Lawrence Forest; Acadian Forest; Boreal Forest. Dotted line indicates the coniferous coastal belt of fir and spruce discussed in text.

MAP 5. The Herpetofaunal Sections of Eastern Canada.

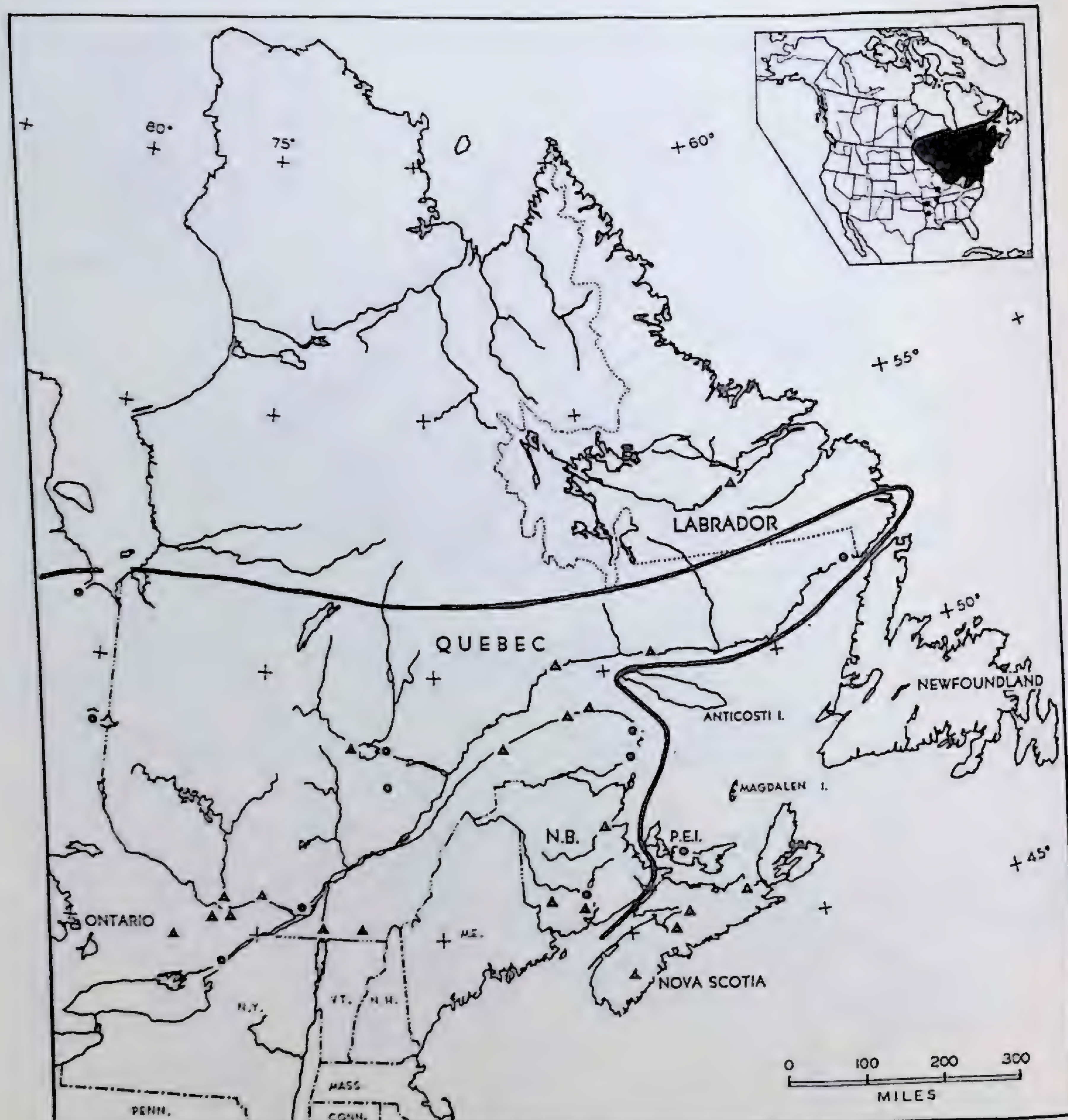


MAP 6. Northern limit lines for the Orders of amphibians and reptiles, and the Garter Snake, in Eastern Canada.

Map 7. Environmental Temperature Indices plotted on a map of the Herpetofaunal Sections of Eastern Canada.

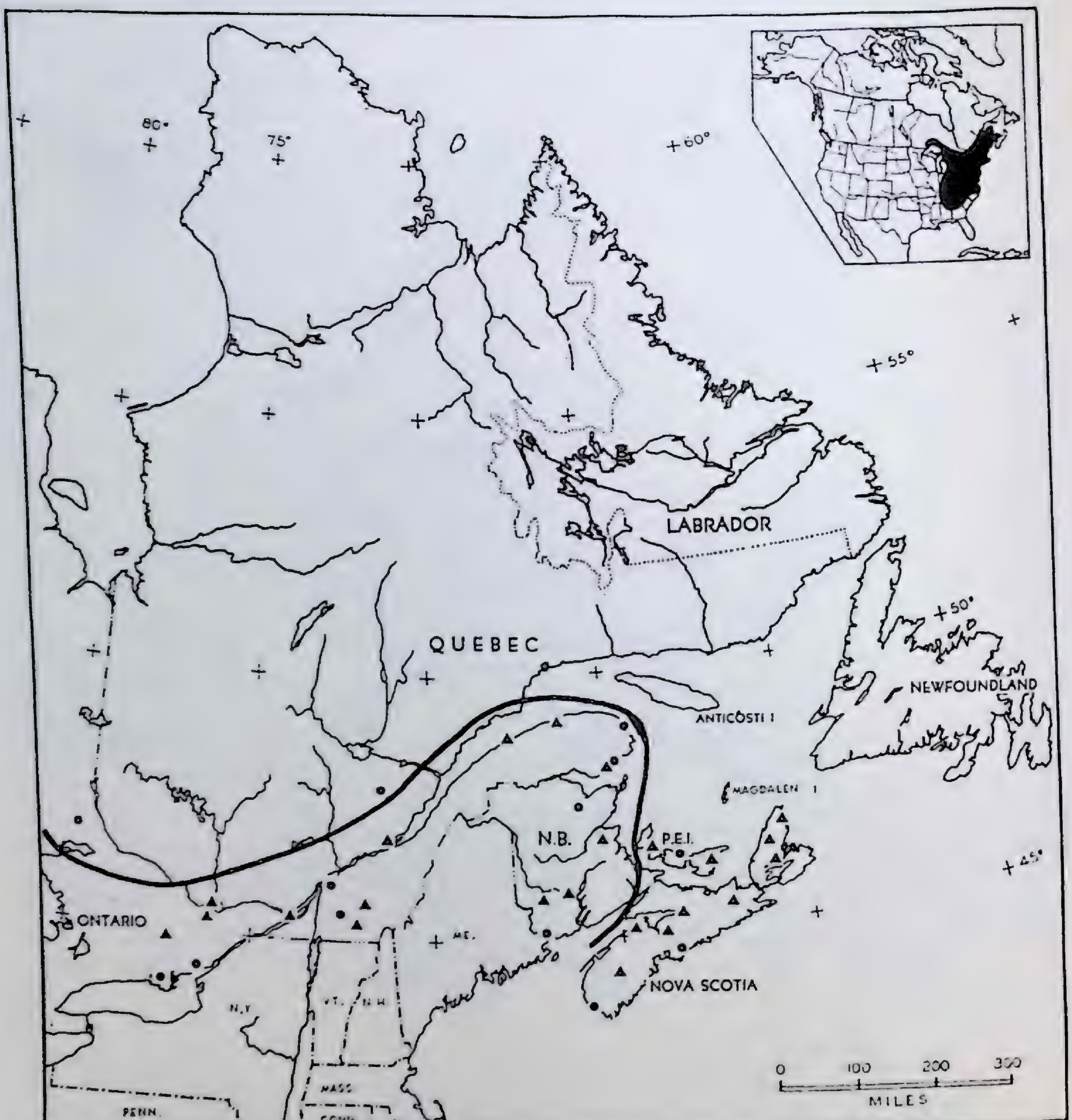


MAP 8. Distributional records of *Necturus maculosus maculosus*. Solid line on map and blackened area on inset map represent range limit of this species according to Bishop, 1947. Explanation of symbols used on distribution maps: Black triangles represent records for which the author is responsible, and black circles represent records reported by other authors; black squares represent rare or dubious reports which are discussed in the text.



MAP 9. Distributional records of *Ambystoma jeffersonianum*. Solid line on map and blackened area on inset map represent range limit of this species according to Bishop, 1947.

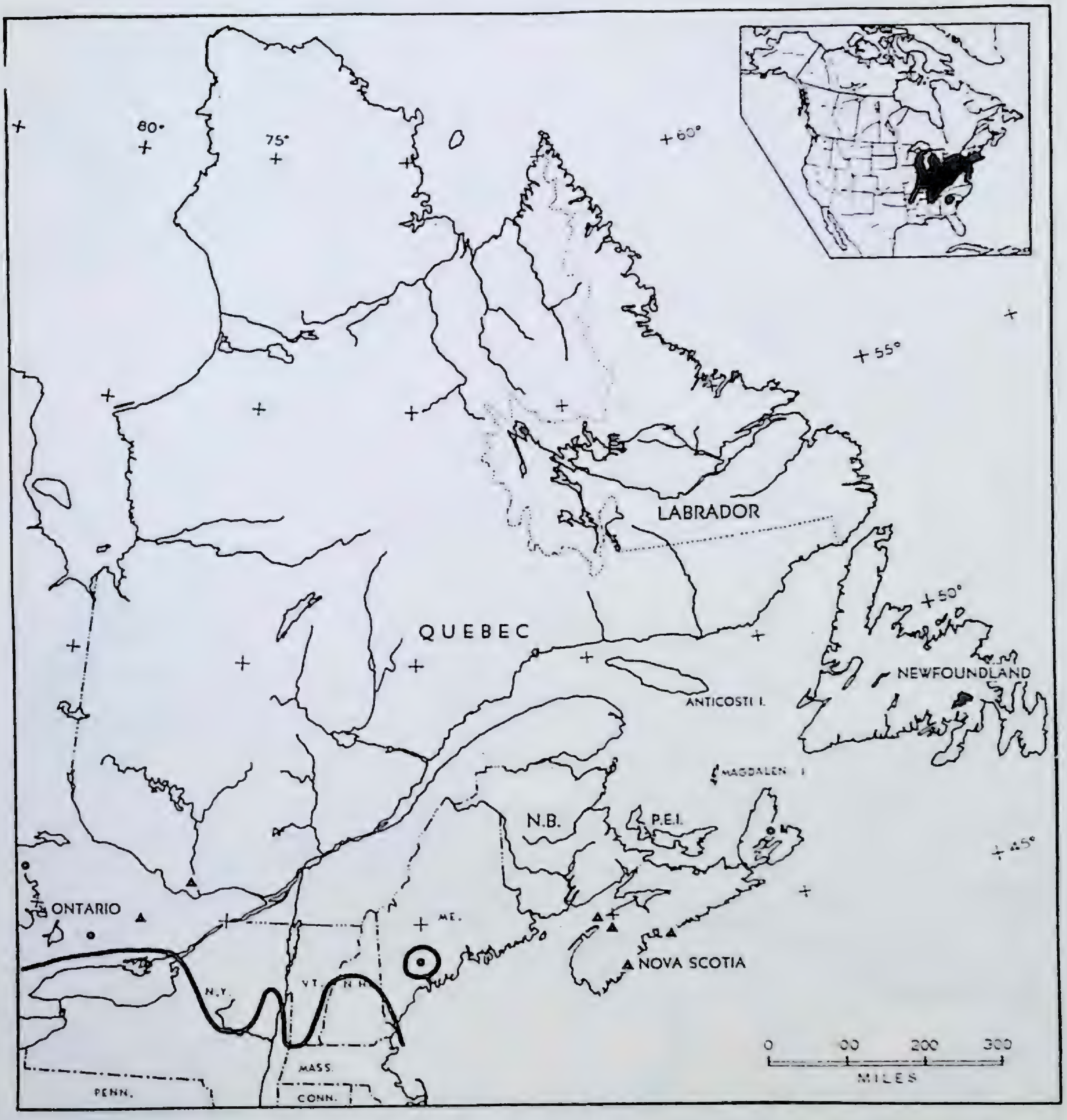
MAP 10. Distributional records of *Ambystoma maculatum*. Solid line on map and blackened area on inset map represent range limit of this species according to Bishop, 1947.



MAP 11. Distributional records of *Diemictylus viridescens viridescens*. Solid line on map and blackened area on inset map represent range limit of this species according to Bishop, 1947.

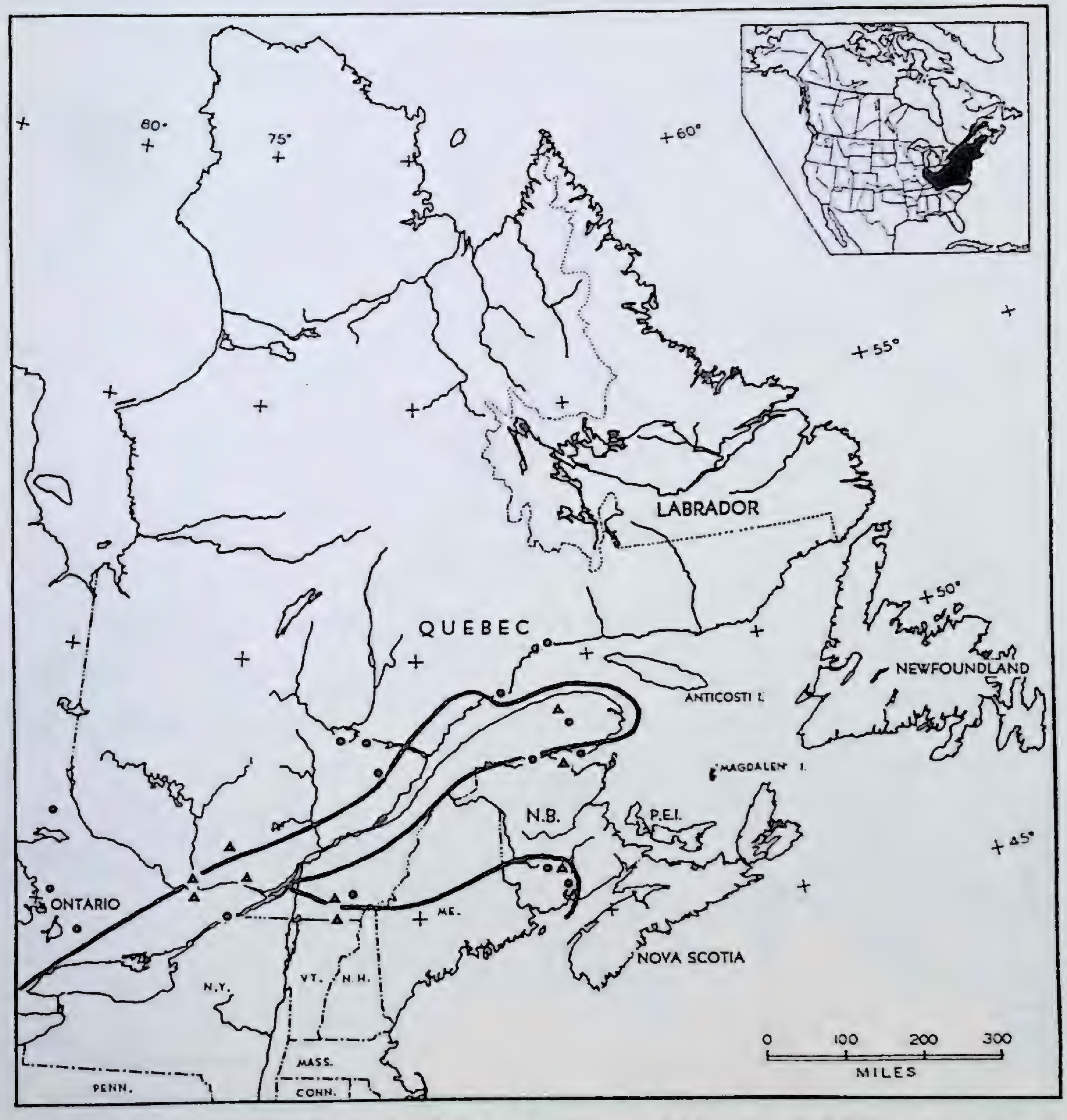
MAP 12. Distributional records of *Desmognathus fuscus fuscus.* Solid line on map and blackened area on inset map represent range limit of this species according to Bishop, 1947.

MAP 13. Distributional records of *Plethodon cinereus cinereus*. Solid line on map and blackened area on inset map represent range limit of this species according to Bishop, 1947.



MAP 14. Distributional records of *Hemidactylium scutatum*. Solid line on map and blackened area on inset map represent range limit of this species according to Bishop, 1947.

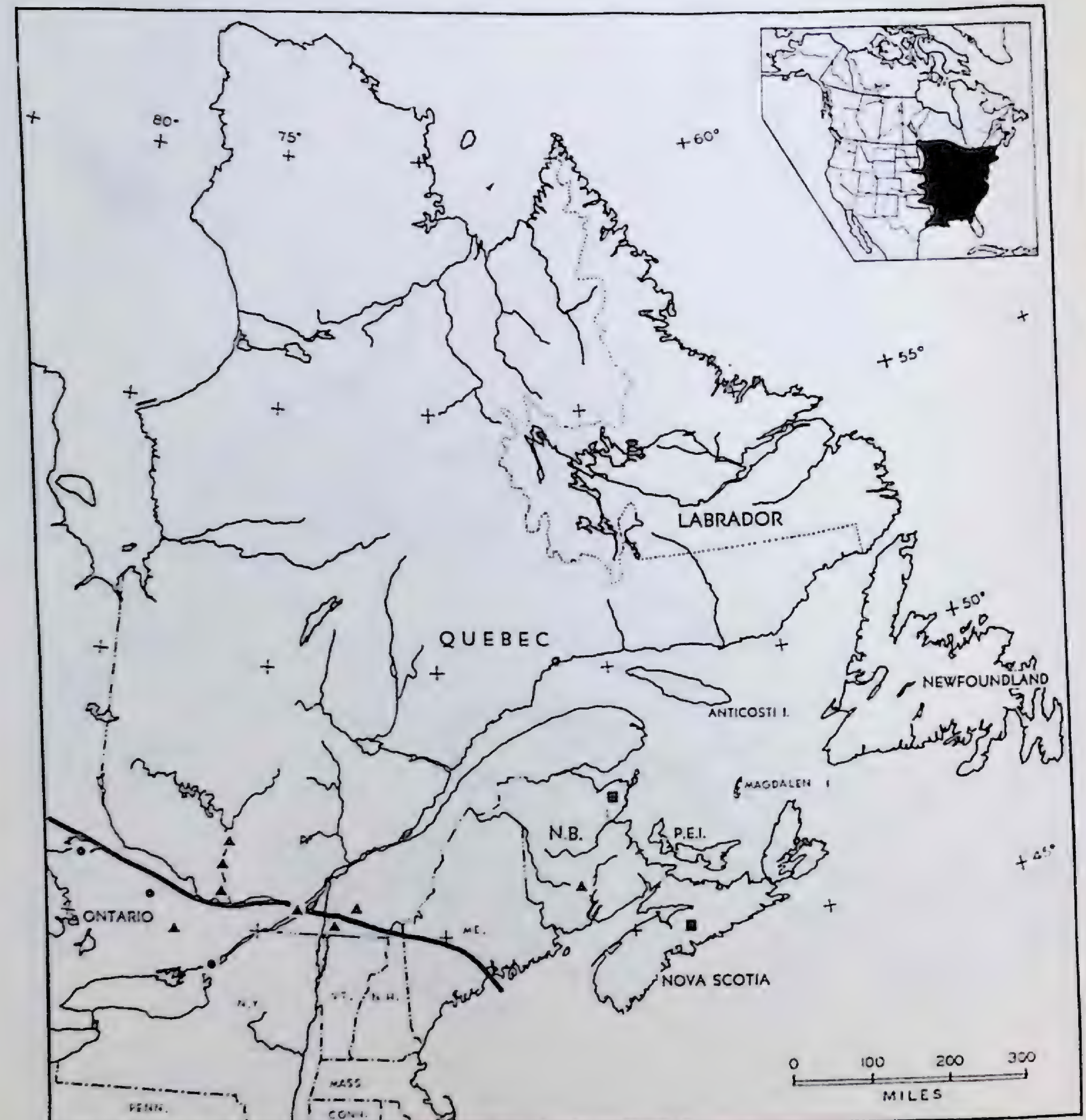
MAP 15. Distributional records of *Gyrinophilus porphyriticus porphyriticus*. Solid line on map and blackened area on inset map represent range limit of this species according to Bishop, 1947.



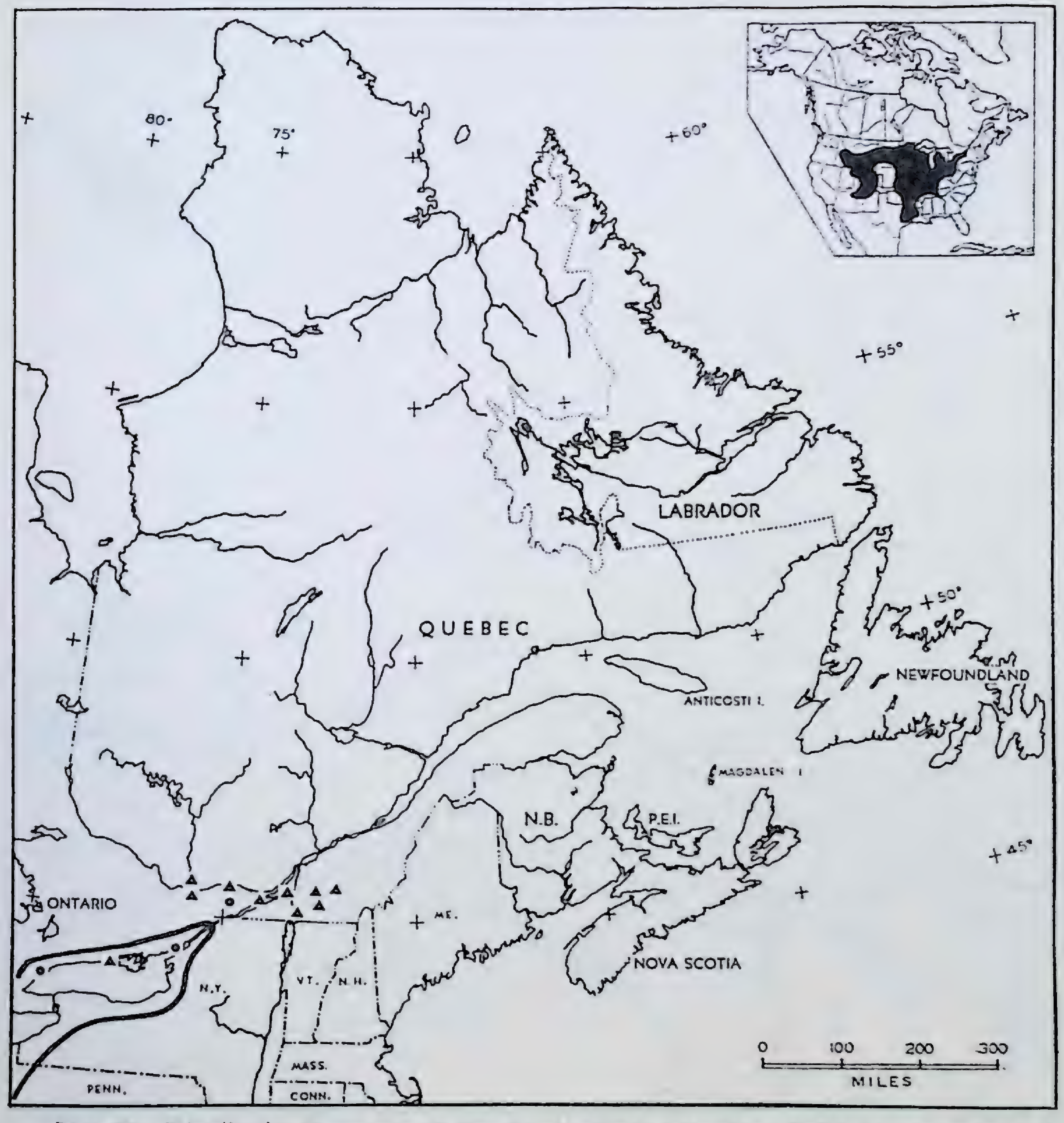
Map 16. Distributional records of *Eurycea bislineata bislineata*. Solid line on map and blackened area on inset map represent range limit of this species according to Bishop, 1947.

MAP 17. Distributional records of *Bufo americanus*. Solid line on map and blackened area on inset map represent range limit of this species according to Wright and Wright, 1949.

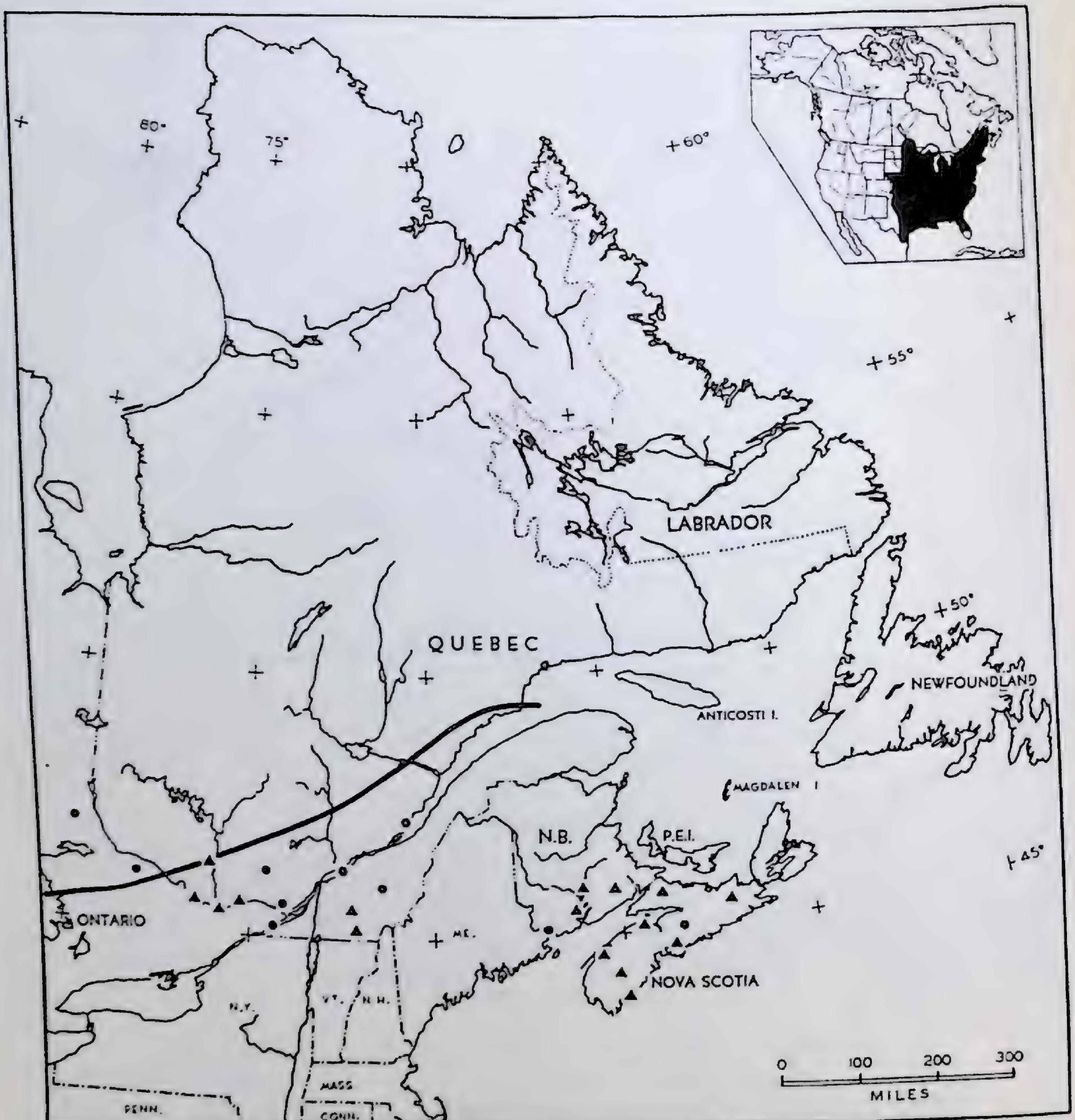
MAP 18. Distributional records of *Hyla crucifer crucifer*. Solid line on map and blackened area on inset map represent range limit of this species according to Wright and Wright, 1949.



MAP 19. Distributional records of *Hyla versicolor versicolor*. Solid line on map and blackened area on inset map represent range limit of this species according to Wright and Wright, 1949.

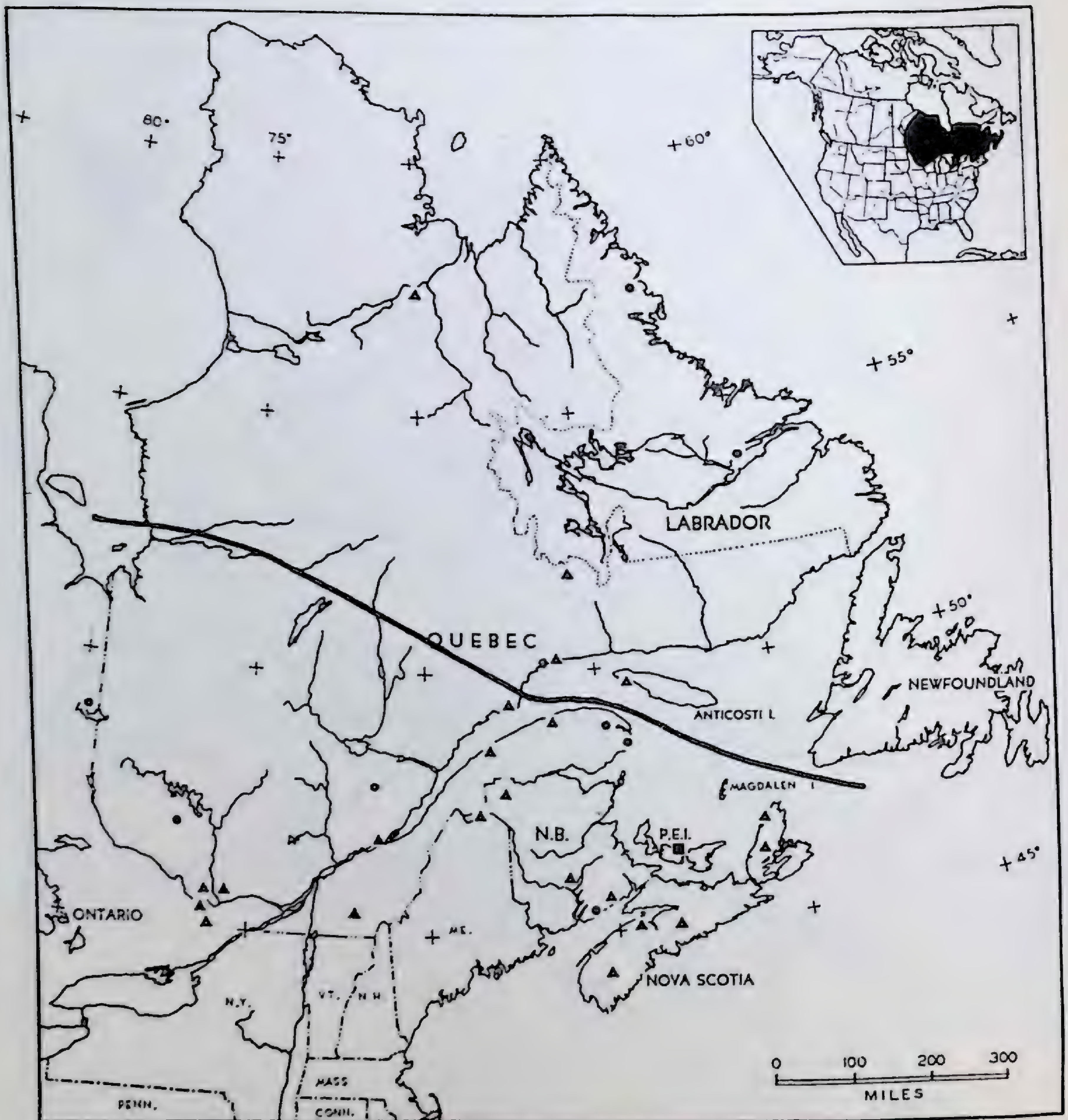


MAP 20. Distributional records of *Pseudacris nigrita triseriata*. Solid line on map and blackened area on inset map represent range limit of this species according to Wright and Wright, 1949.

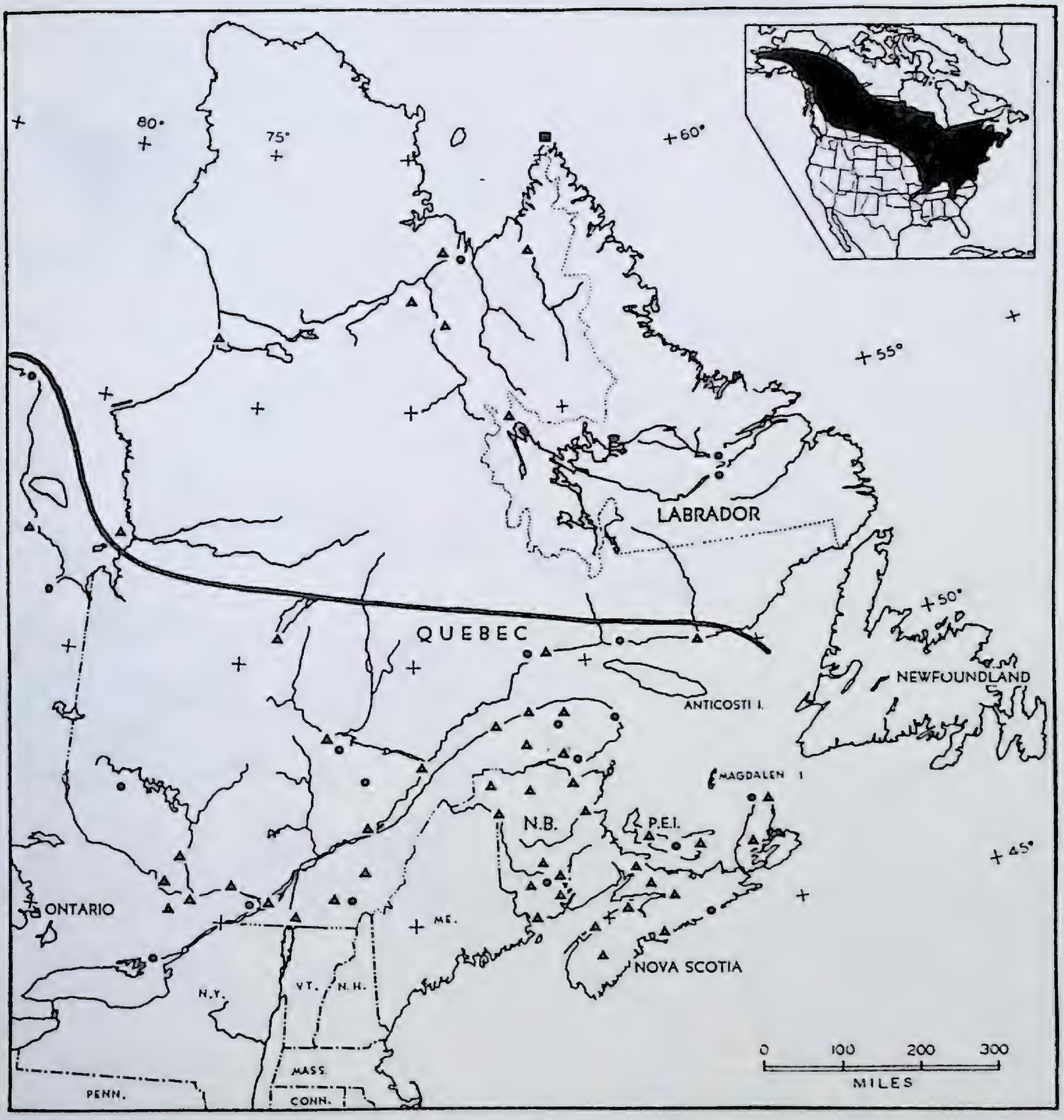


MAP 21. Distributional records of *Rana catesbeiana*. Solid line on map and blackened area on inset map represent range limit of this species according to Wright and Wright, 1949.

MAP 22. Distributional records of *Rana clamitans*. Solid line on map and blackened area on inset map represent range limit of this species according to Wright and Wright, 1949.



MAP 23. Distributional records of *Rana septentrionalis.* Solid line on map and blackened area on inset map represent range limit of this species according to Wright and Wright, 1949.



MAP 24. Distributional records of *Rana sylvatica*. Solid line on map and blackened area on inset map represent range limit of this species according to Wright and Wright, 1949.

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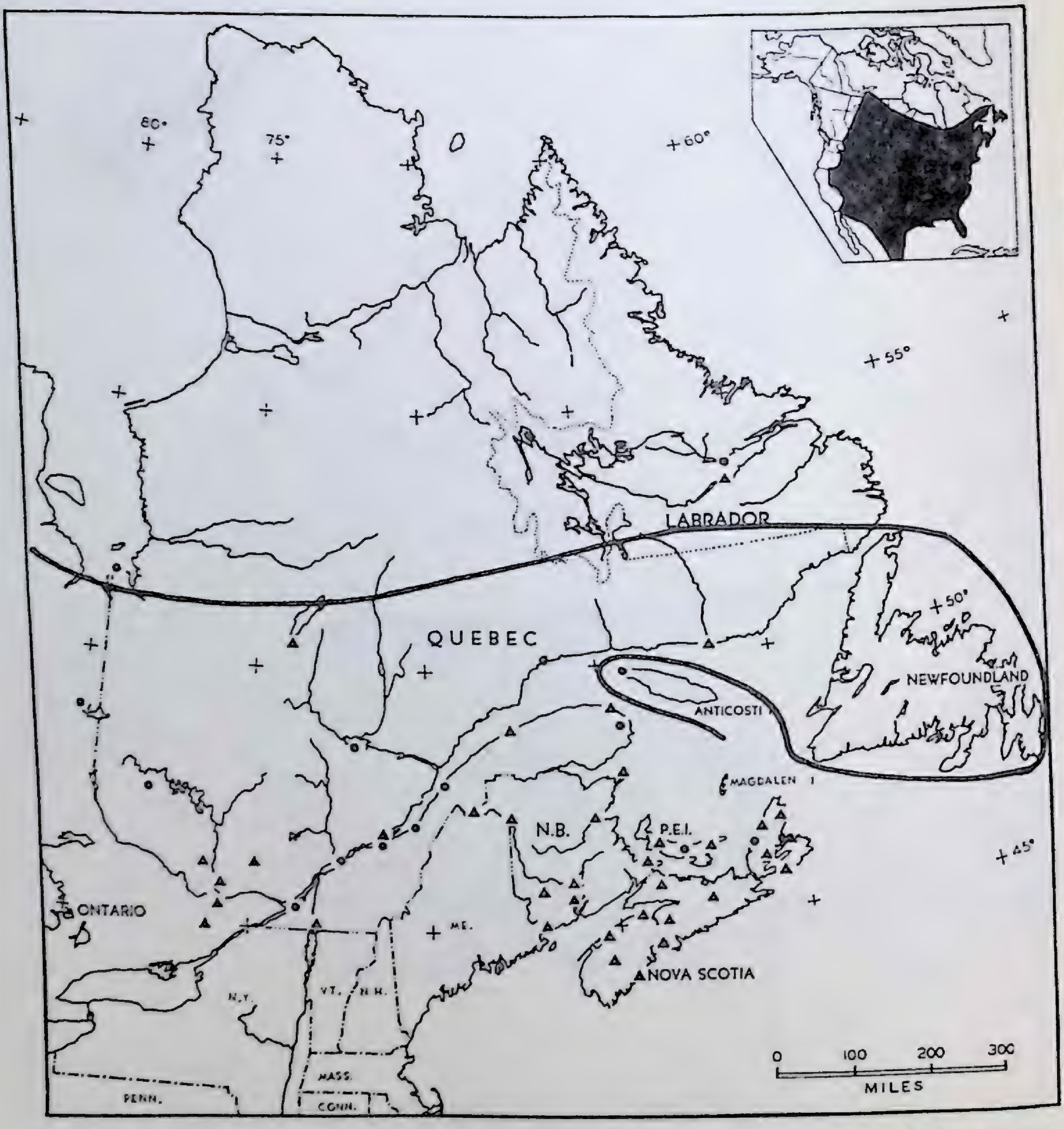
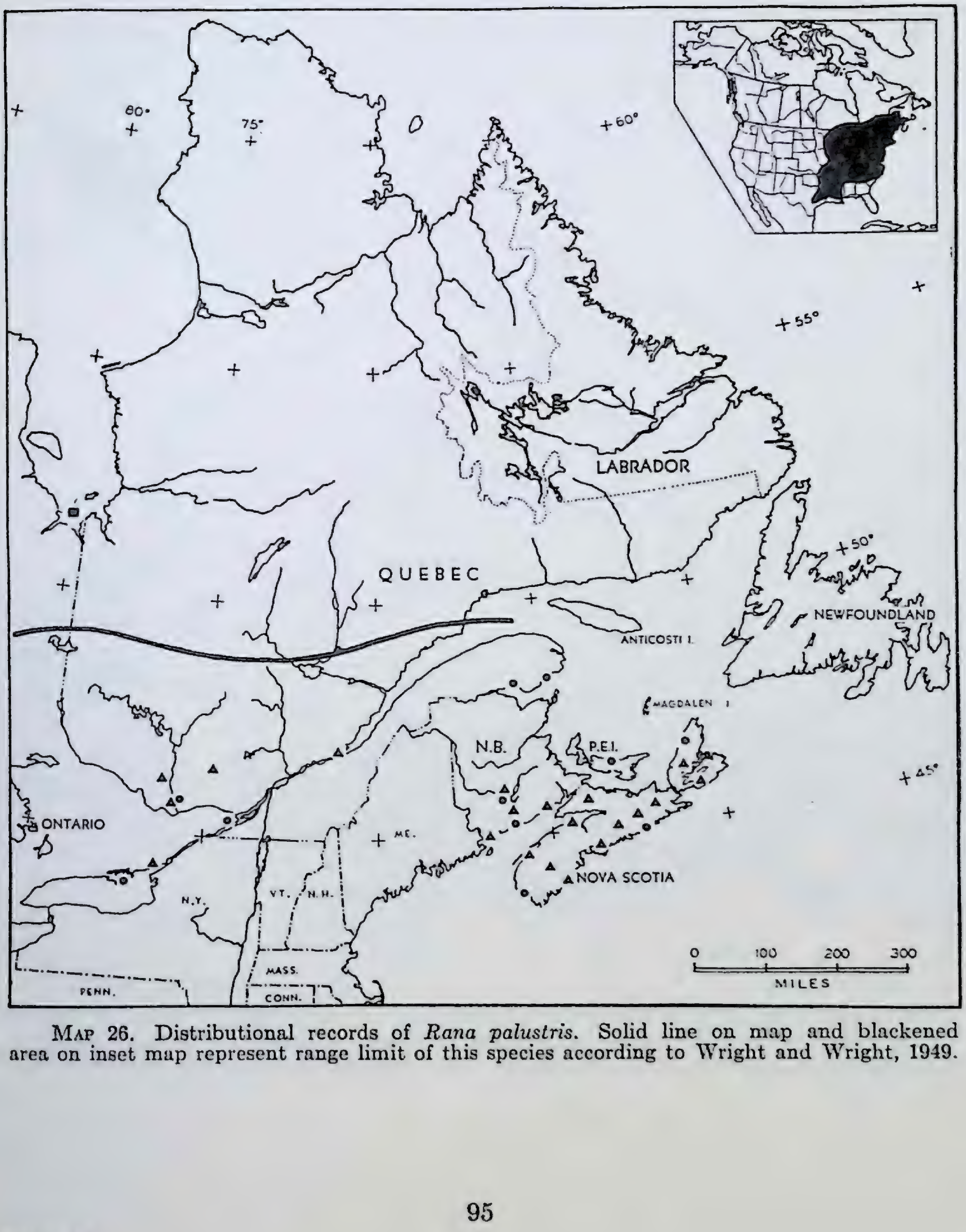
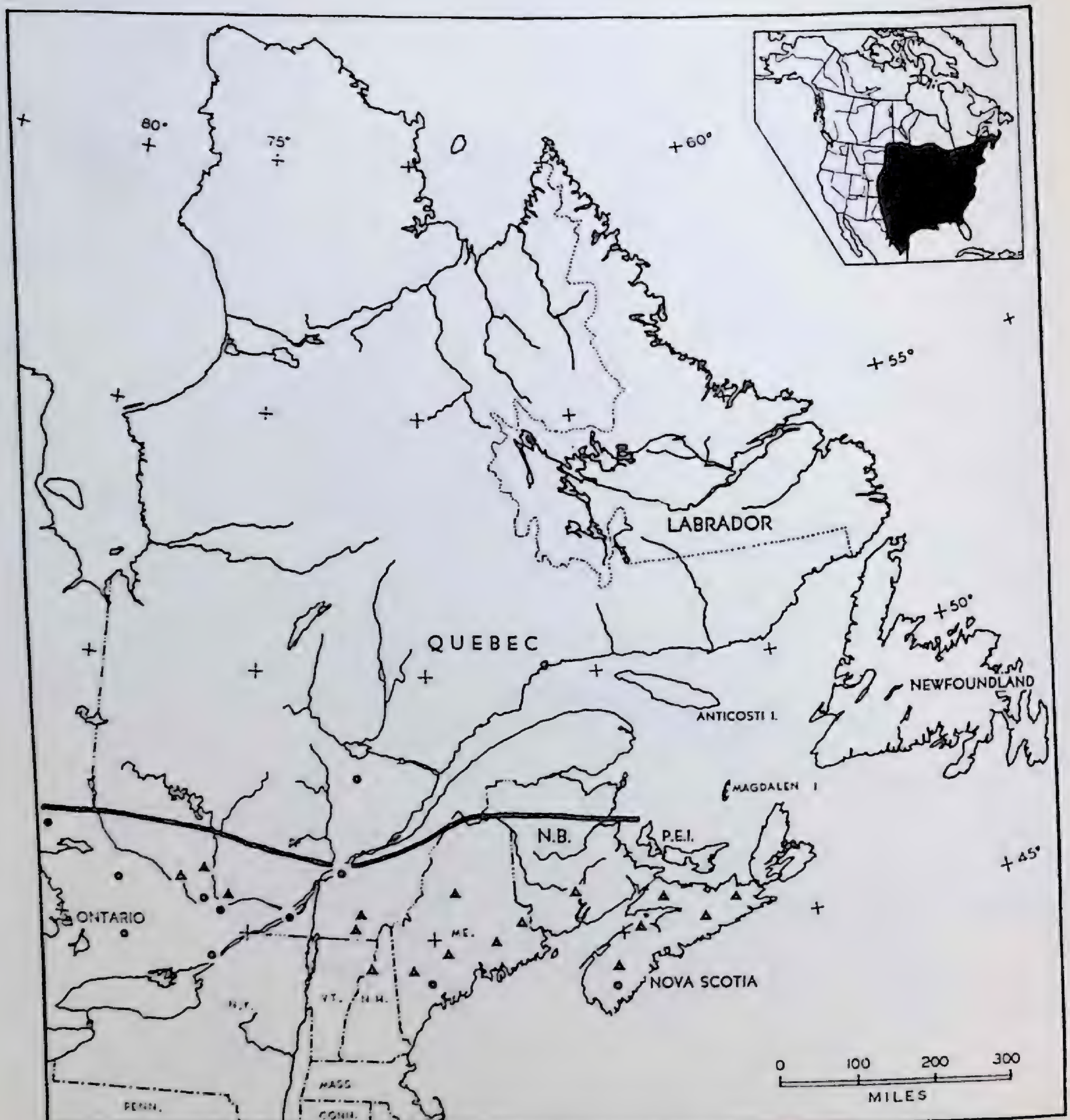


MAP 25. Distributional records of *Rana pipiens*. Solid line on map and blackened area on inset map represent range limit of this species according to Wright and Wright, 1949.



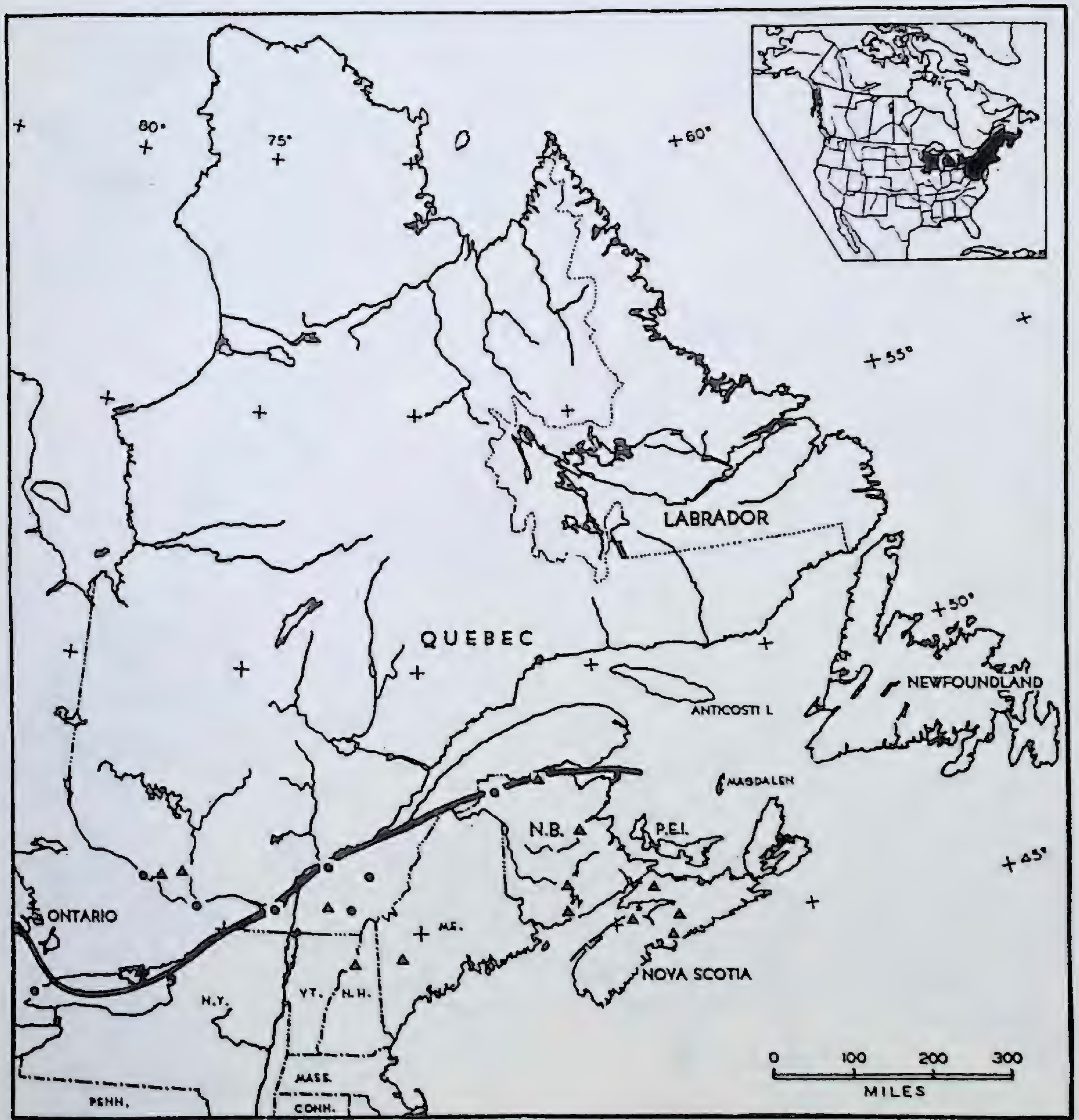
MAP 26. Distributional records of *Rana palustris*. Solid line on map and blackened area on inset map represent range limit of this species according to Wright and Wright, 1949.



Map 27. Distributional records of *Chelydra serpentina serpentina*. Solid line on map and blackened area on inset map represent range limit of this species according to Carr, 1952.

MAP 28. Distributional records of *Sternotherus odoratus*. Solid line on map and blackened area on inset map represent range limit of this species according to Carr, 1952.

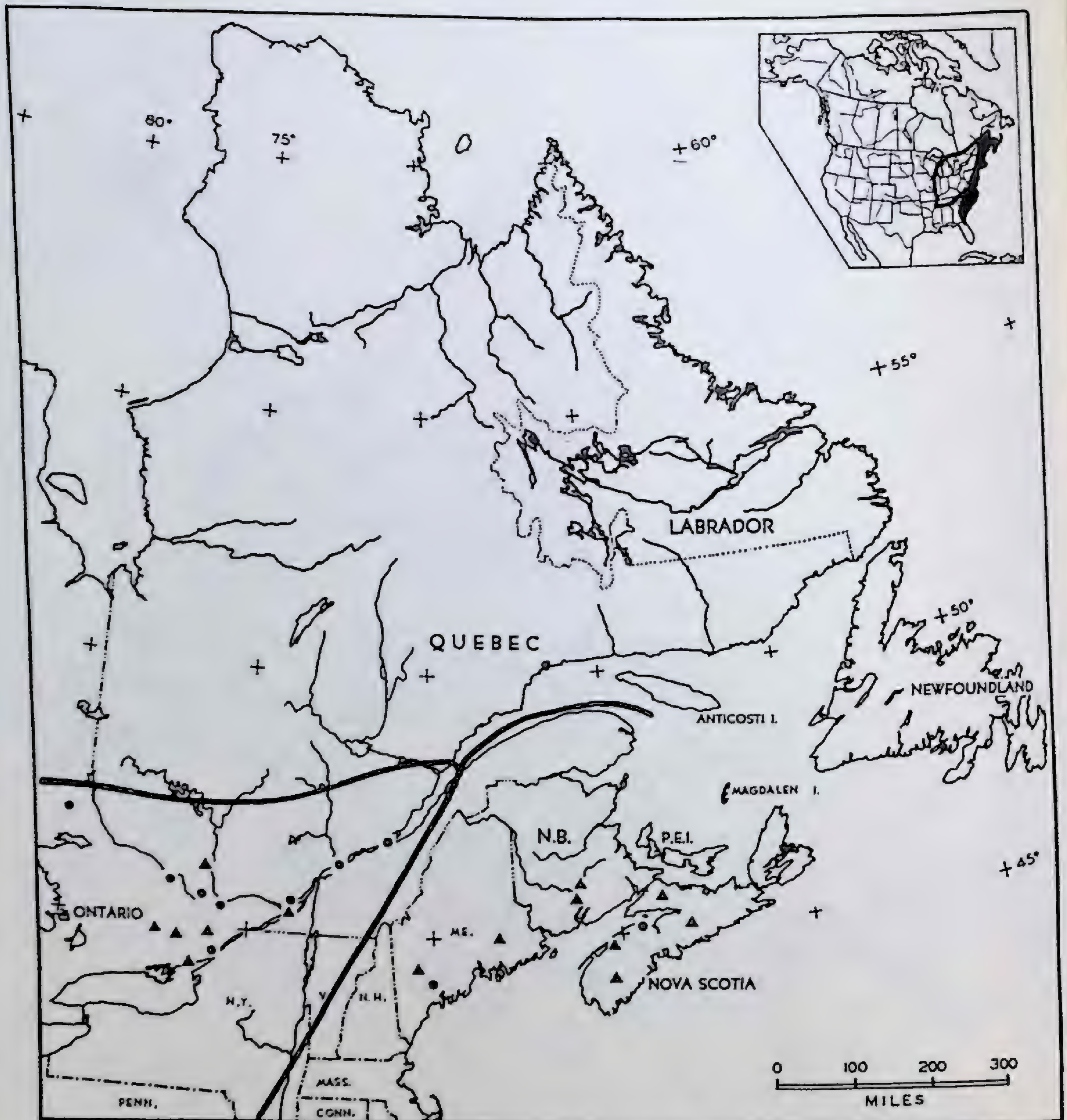
MAP 29. Distributional records of *Clemmys guttata*. Solid line on map and blackened area on inset map represent range limit of this species according to Carr, 1952.



Map 30. Distributional records of *Clemmys insculpta*. Solid line on map and blackened area on inset map represent range limit of this species according to Carr, 1952.

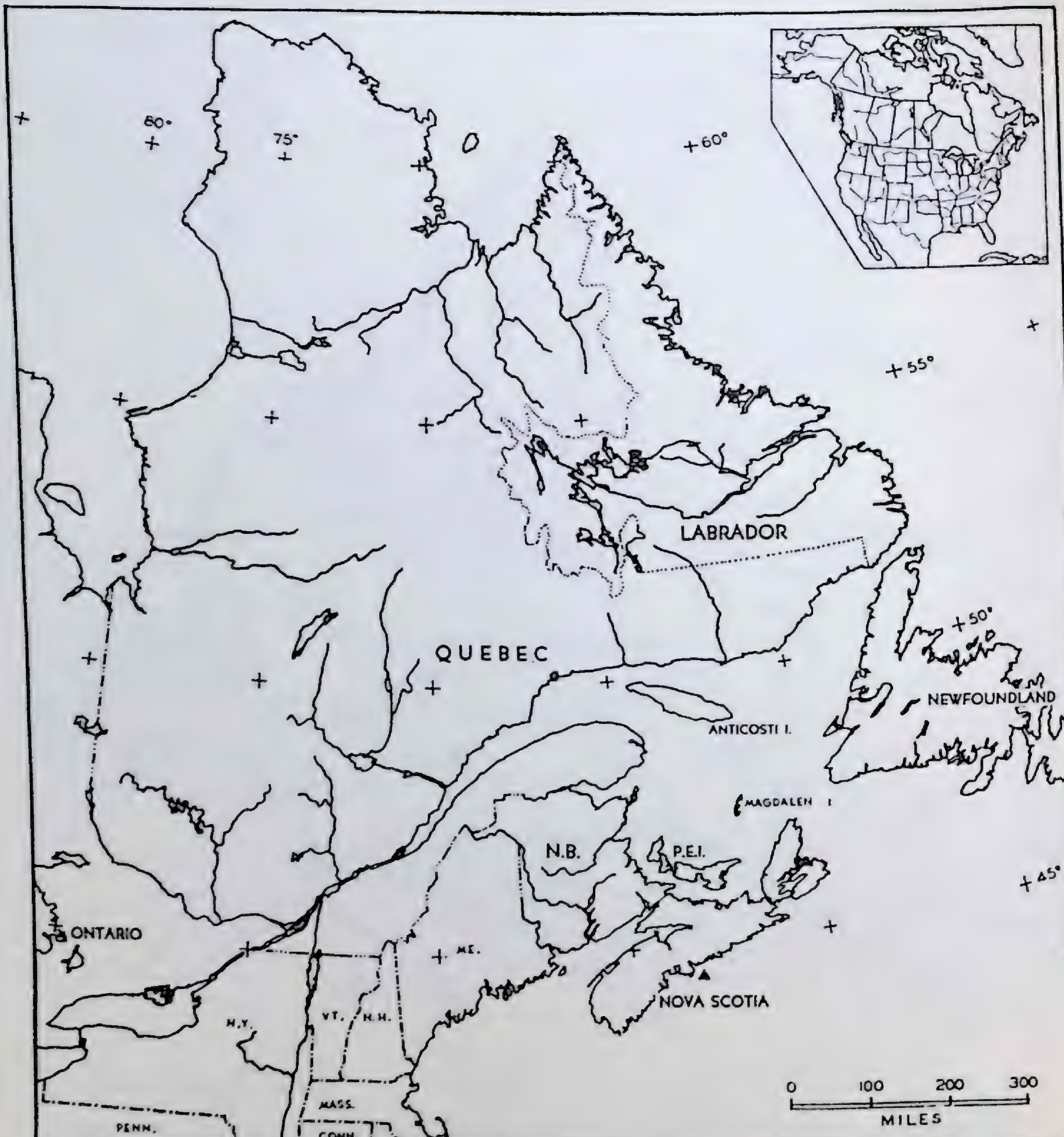
MAP 31. Distributional records of *Emys blandingi*. Solid line on map and blackened area on inset map represent range limit of this species according to Carr, 1952.

MAP 32. Distributional records of *Graptemys geographica*. Solid line on map and blackened area on inset map represent range limit of this species according to Carr, 1952.



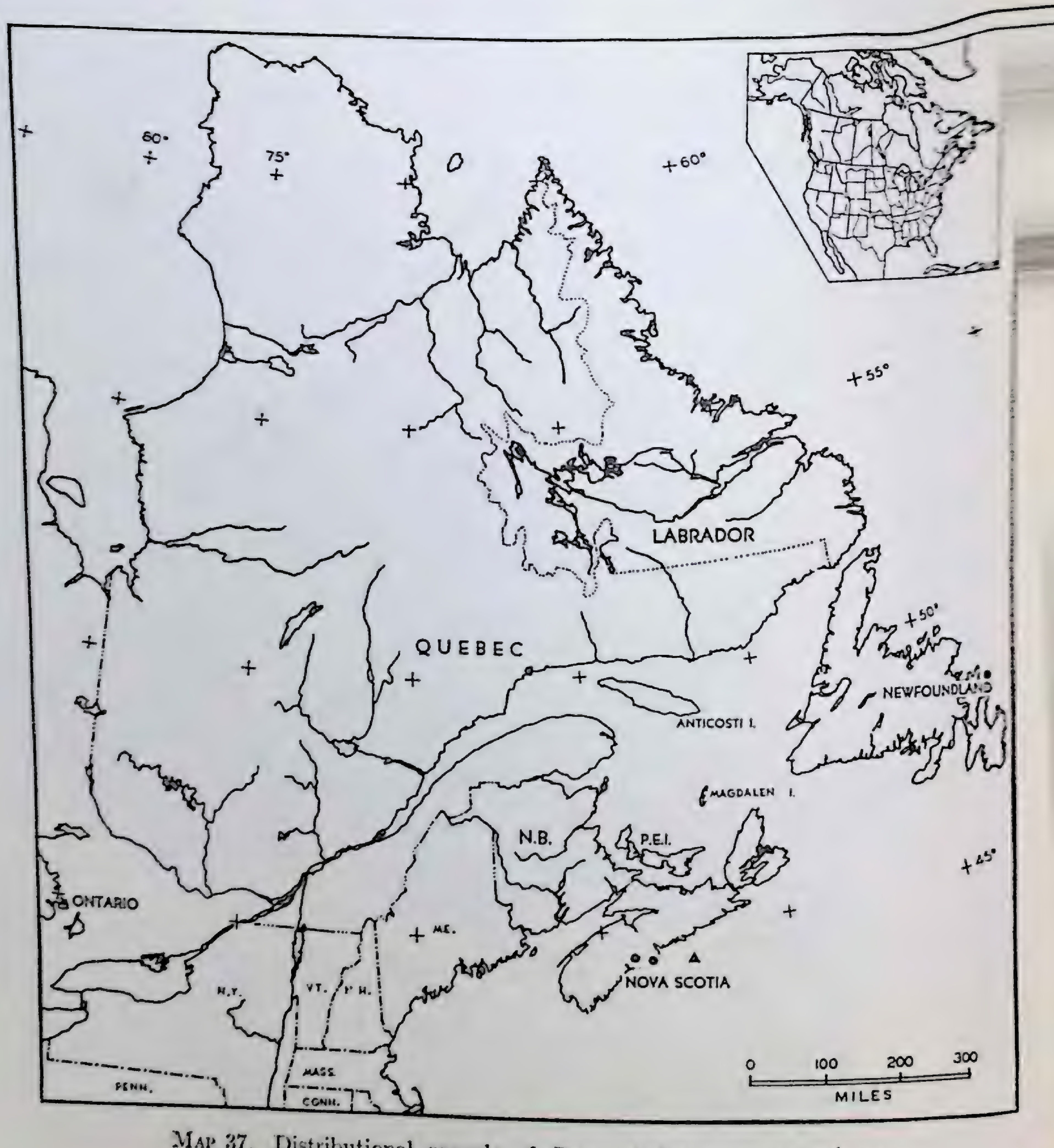
MAP 33. Distributional records of *Chrysemys picta marginata* and *C. p. picta*. Solid line on map represents range limit of these two subspecies according to Carr, 1952. Encircled area on inset map depicts range of *C. p. marginata*, and blackened area depicts range of *C. p. picta* according to Carr, 1952.

MAP 34. Distributional records of *Lepidochelys olivacea kempi.*



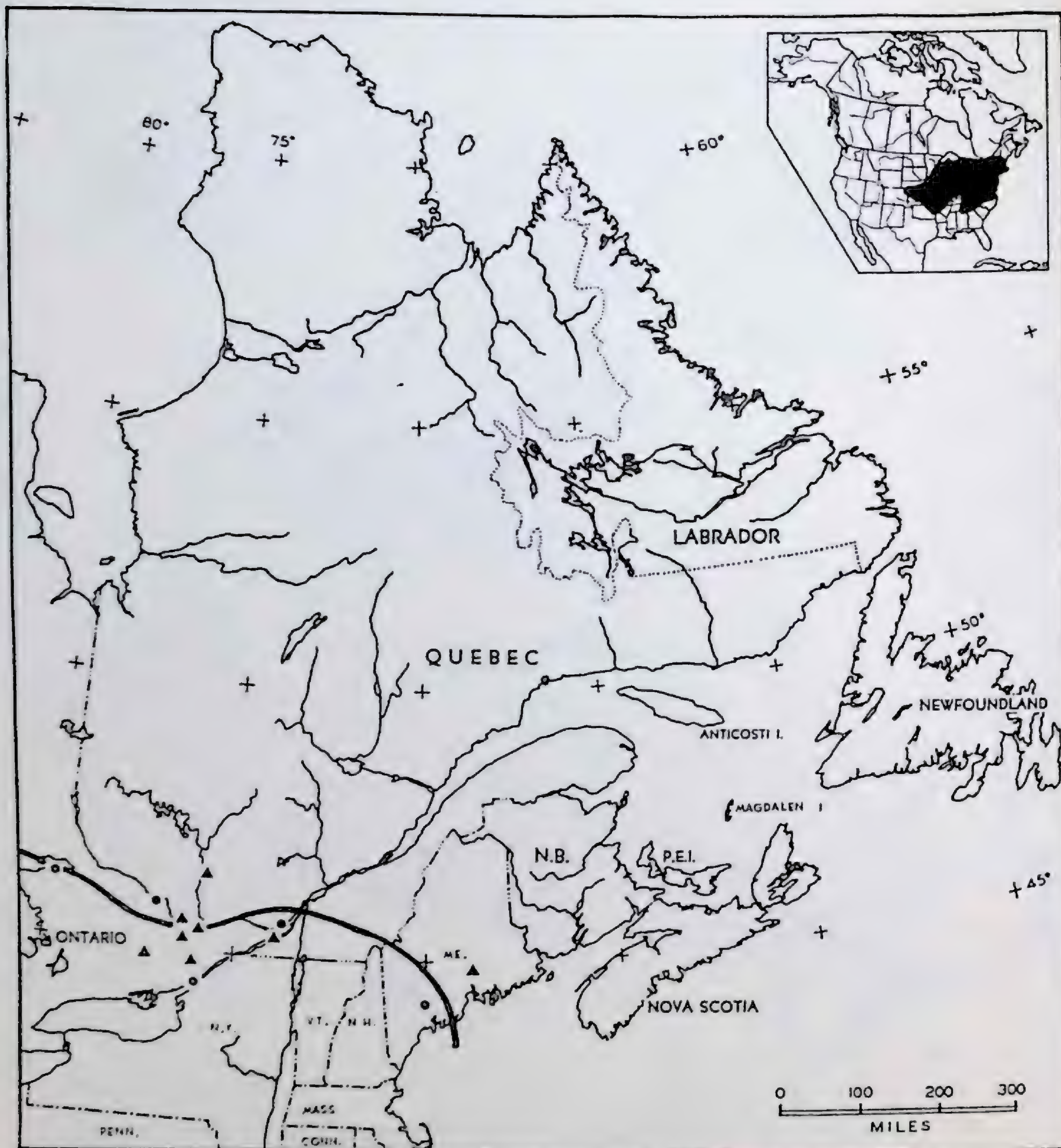
Map 35. Distributional records of *Caretta caretta caretta*.

MAP 36. Distributional records of *Trionyx ferox spinifera*. Solid line on map and blackened area on inset map represent range limit of this species according to Carr, 1952.

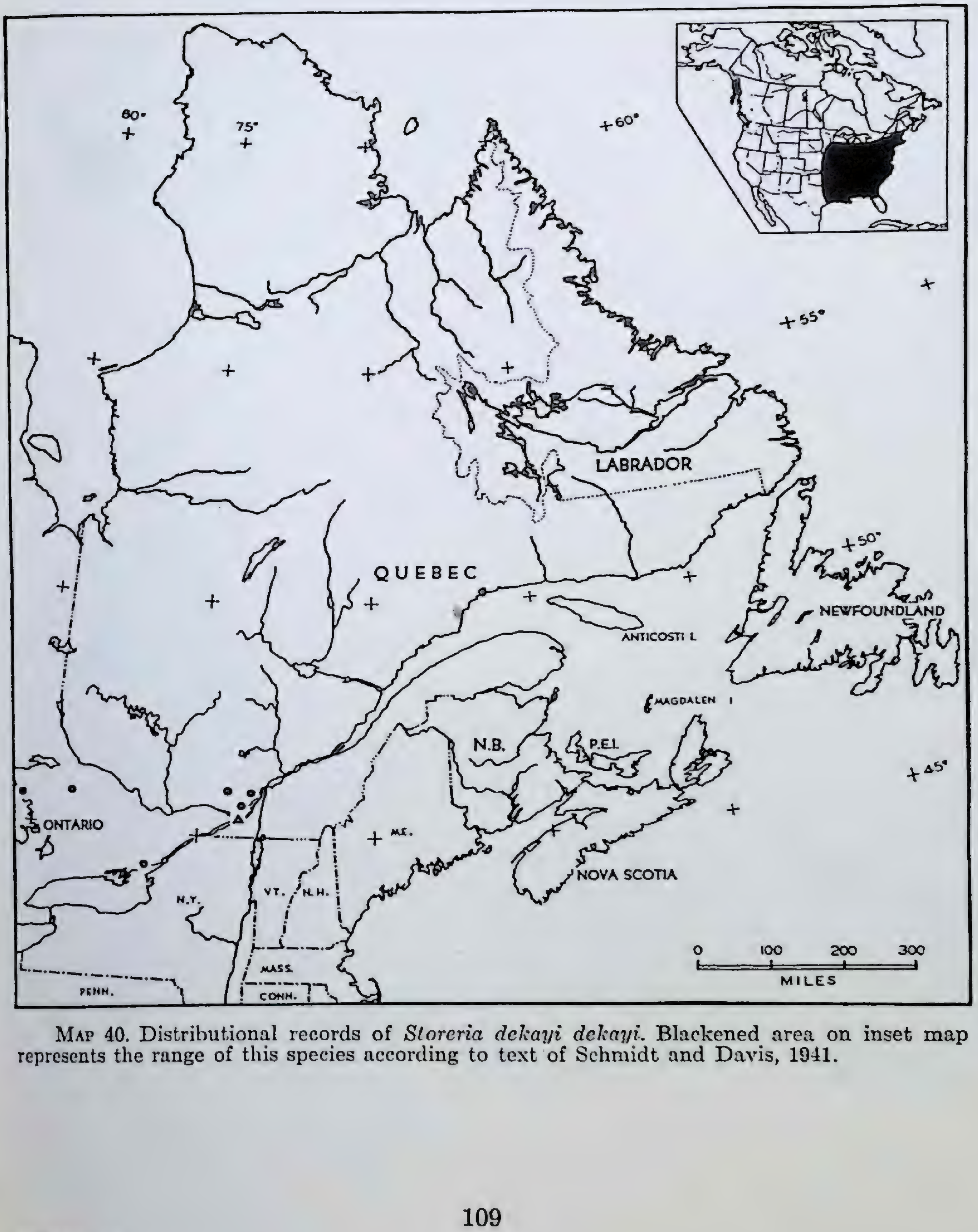


MAP 37. Distributional records of *Dermochelys coriacea coriacea.*

MAP 38. Distributional records of *Eumeces fasciatus*. Solid line on map and blackened area on inset map represent range limit of this species according to Fitch, 1954.



MAP 39. Distributional records of *Natrix sipedon sipedon*. Solid line on map and blackened area on inset map represent range limit of this species according to Schmidt and Davis, 1941.



Map 40. Distributional records of *Storeria dekayi dekayi*. Blackened area on inset map represents the range of this species according to text of Schmidt and Davis, 1941.

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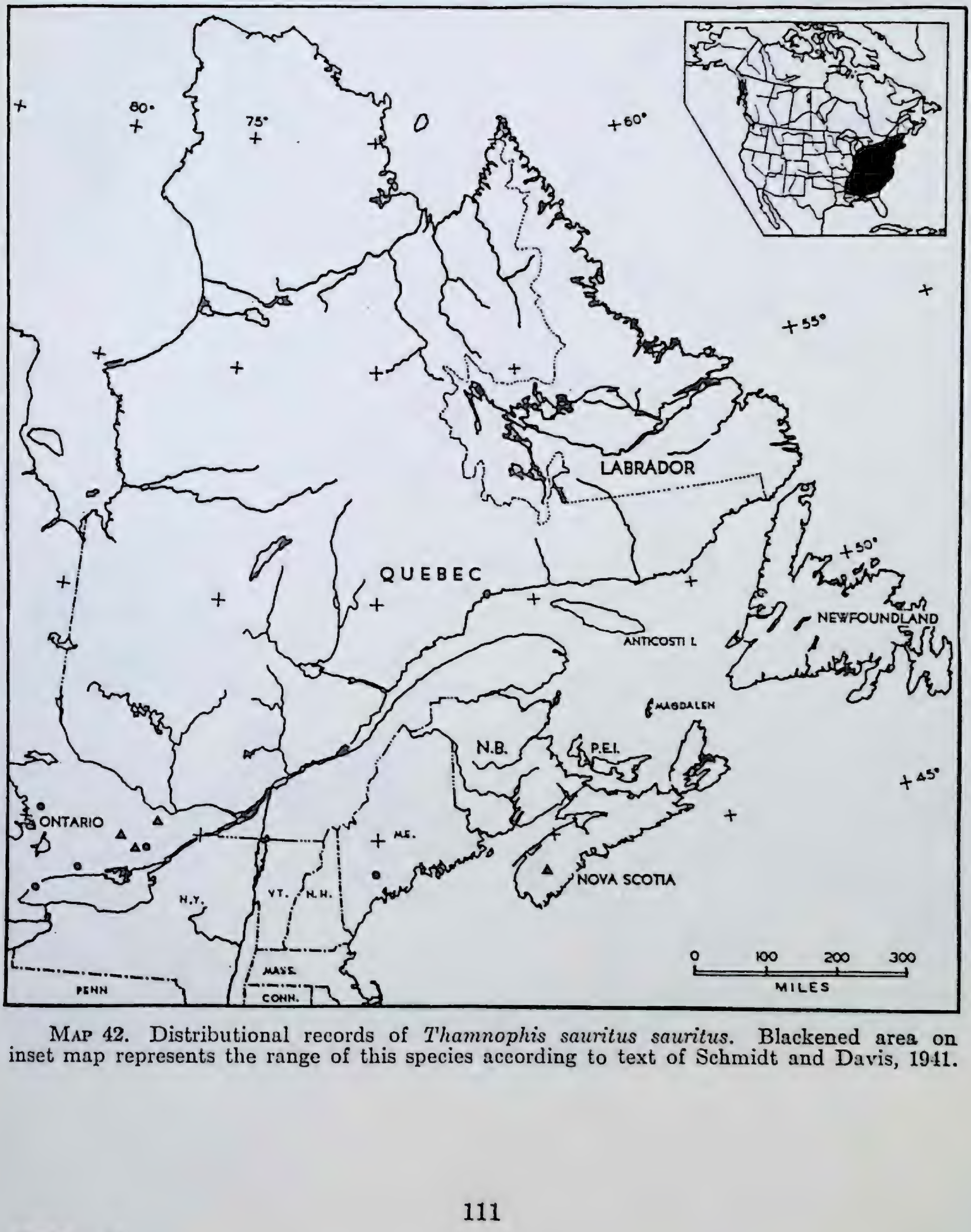
MAP 41. Distributional records of *Storeria occipitomaculata occipitomaculata*. Blackened area on inset map represents the range of this species according to text of Schmidt and Davis, 1941.



MAP 42. Distributional records of *Thamnophis sauritus sauritus*. Blackened area on inset map represents the range of this species according to text of Schmidt and Davis, 1941.

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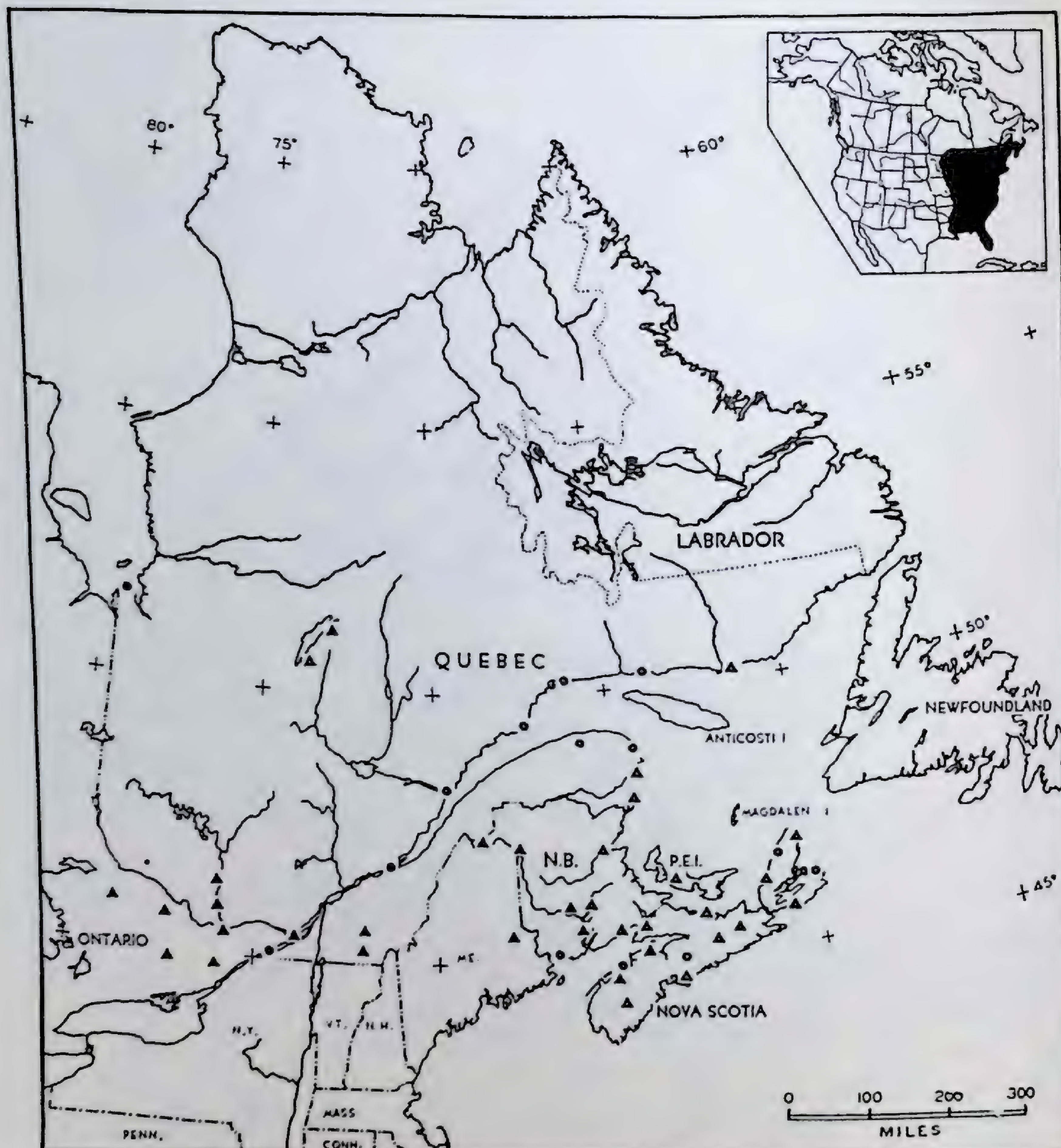
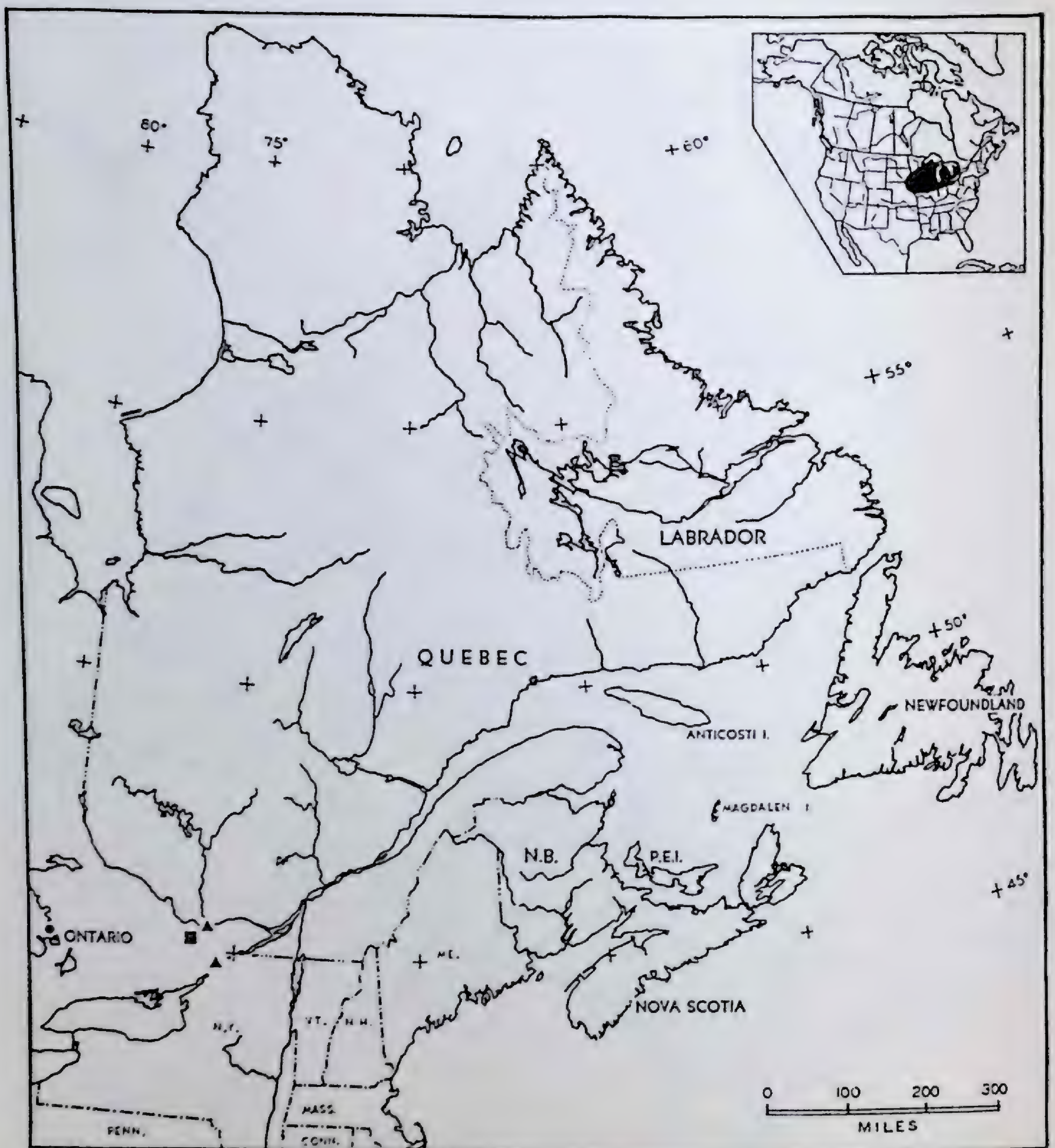


MAP 43. Distributional records of *Thamnophis sirtalis sirtalis*. Blackened area on inset map represents the range limit of this species according to text of Schmidt and Davis, 1941.

Map 44. Distributional records of *Diadophis punctatus edwardsi*. Blackened area on inset map represents the range limit of this species according to text of Schmidt and Davis, 1941.

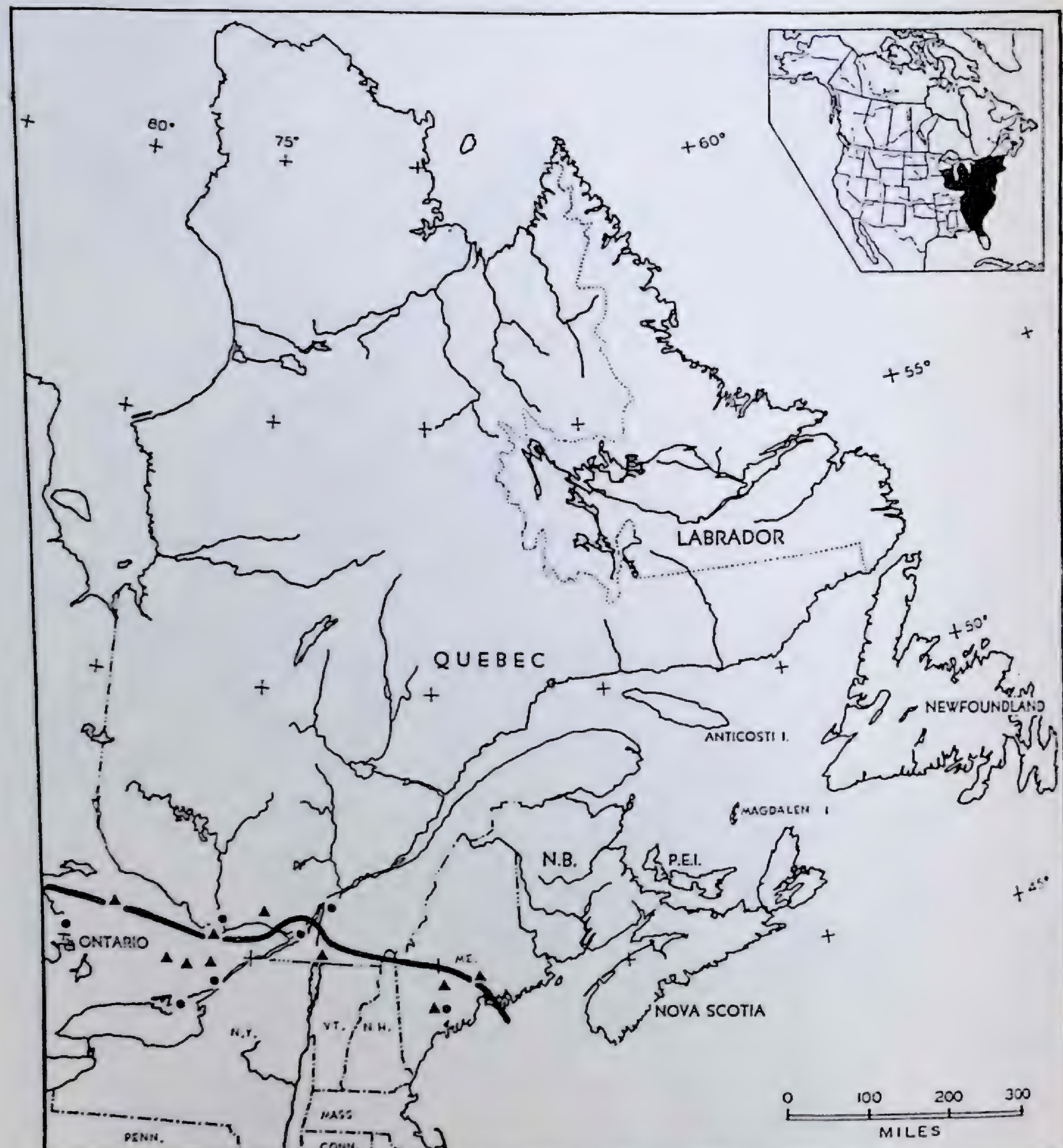
MAP 45. Distributional records of *Coluber constrictor constrictor*. Blackened area on inset map represents the range limit of this species according to text of Schmidt and Davis, 1941.

MAP 46. Distributional records of *Opheodrys vernalis vernalis*. Blackened area on inset map represents the range limit of this species according to text of Schmidt and Davis, 1941.



MAP 47. Distributional records of *Elapho vulpina*. Blackened area on inset map represents the range limit of this species according to text of Schmidt and Davis, 1941.

Map 48. Distributional records of *Elapho obsoleta obsoleta*. Blackened area on inset map represents the range limit of this species according to text of Schmidt and Davis, 1941.



MAP 49. Distributional records of *Lampropeltis doliata triangulum*. Solid line on map and blackened area on inset map represent range limit of this species according to Schmidt and Davis, 1941.

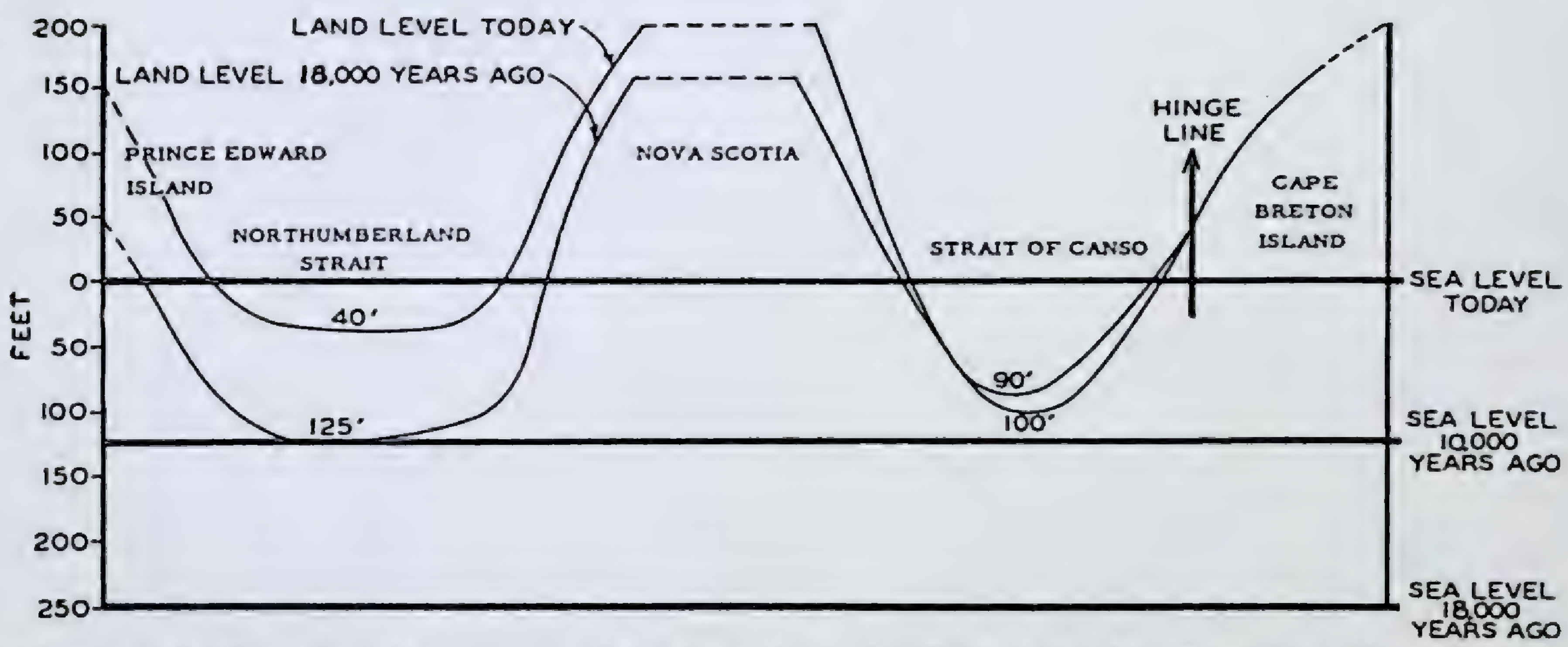


Diagram 1. Postglacial sequence of land- and sea-level changes demonstrating the existence of land bridges in early postglacial times.